

A PHYLOGENETIC STUDY OF THE HORNED LIZARDS, GENUS *PHRYNOSOMA*, BASED ON SKELETAL AND EXTERNAL MORPHOLOGY

Richard R. Montanucci¹

ABSTRACT. The phylogenetic relationships among the species of *Phrynosoma* were determined through computer analysis of 36 external and osteological characters. Phylogenetic Analysis Using Parsimony (PAUP, Version 2.4) produced a cladogram that depicts two major phyletic lines diverging from a common ancestor. One line gave rise to the "southern radiation" species, including *P. asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*. The other produced a "northern radiation" group containing *P. douglassii*, *P. cornutum*, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, and *P. solare*. This arrangement differs in several ways from a previously hypothesized phylogeny (Presch, 1969). *Phrynosoma asio* and *P. orbiculare* have relatively more plesiomorphic characters than the other species within their respective groups. *Phrynosoma ditmarsii* is not close to *P. douglassii*, but is a descendant of an *asio*-like progenitor. It is distantly related to the southern species, *P. braconneri* and *P. taurus*, with which it shares similarities in lepidosis and habitus, all three being relatively long-limbed, short-tailed, upland *Phrynosoma*. The desert species derived from a *coronatum*-like progenitor did not diverge as a polytomy, but as a series of sequential branchings. *Phrynosoma modestum* and *P. mcallii* are not sister species. Instead, *P. modestum* and *P. platyrhinos* are sister taxa sharing a most recent common ancestor. *Phrynosoma mcallii* represents the sister taxon of both species. A computer-generated patristic distance tree reveals that most members of the northern radiation group have undergone considerable anagenetic evolutionary change compared with the southern group members, which are less evolved from the common ancestor. The southern group species comprise a relictual assemblage, and speciation within the southern group may have predated most of the diversification of the northern group.

A study of the character patterns reveals some striking examples of homoplastic similarity between some members of the two groups. The convergent characters involve: 1) the spatial arrangement of the nasal, maxillary, and prefrontal elements; 2) the position and angle of entry of the external nares; 3) the extent of overlap of the coronoid with the dentary and surangular; 4) the formation of a complete supraorbital bar; 5) the extent of development of parietal and squamosal horns; 6) the extent of participation of the maxilla in the orbital border; 7) the degree of expansion of the ectopterygoid; 8) the orientation of the supraoccipital; 9) the orientation of the post-orbital; 10) the length of the second ceratobranchials; 11) the number of caudal vertebrae; 12) the development and number of enlarged

gular rows; and 13) the number of lateral abdominal fringe scale rows.

A scenario of the evolutionary history of *Phrynosoma* is developed from published paleogeographic and paleoecological models. Fossil evidence is fragmentary and provides no empirical support for the cladogram. The late Pliocene *Phrynosoma holmani* has an angular dentary which is considered a synapomorphy for *P. cornutum* and its relatives. The Pleistocene *Phrynosoma josecitense*, although not closely related to *P. solare*, defies placement; it appears to be allied to *P. coronatum* or *P. orbiculare*.

Phrynosoma and the sand lizard assemblage (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*) are sister groups within the sceloporines. The sand lizard-*Phrynosoma* clade is supported by a number of synapomorphies, including five osteological characters (Presch, 1969; de Queiroz, 1982) and one myological character (Arnold, 1984). An additional four myological features may be shared between the two groups (Blackburn, unpubl. data). Externally, both *Phrynosoma* and the sand lizard group have tilted supralabials. Moreover, *Phrynosoma* has a series of chinshields which enlarge posteriorly, and these may be homologous to a series of sublabials which also enlarge posteriorly in the sand lizards. Horned lizards comprise a morphologically unique group, distinct from all other sceloporines.

Resumen. Las relaciones filogenéticas entre las especies de *Phrynosoma* se determinaron a través de análisis computacional de 36 caracteres externos y osteológicos. Un cladograma (PAUP; Phylogenetic Analysis Using Parsimony, Versión 2.4) describe dos líneas filéticas mayores que divergen de un ancestro común. Una línea dio origen a las especies de la "radiación sur" incluyendo *P. asio*, *P. braconneri*, *P. ditmarsii*, y *P. taurus*. La otra produjo un grupo de "radiación norte" que contiene *P. douglassii*, *P. cornutum*, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, y *P. solare*. Esta disposición difiere en algunas formas de una filogenia previamente hipotetizada (Presch, 1969). *Phrynosoma asio* y *P. orbiculare* tienen relativamente mas caracteres plesiomórficos que las otras especies dentro de sus respectivos grupos. *Phrynosoma ditmarsii*

1. Department of Biological Sciences, Clemson University, Clemson, South Carolina 29634-1903. Research Associate, Section of Herpetology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.

no está junto a *P. douglassii*, pero es un descendiente de un progenitor como *P. asio*; está relacionada distantemente con las especies del sur, *P. braconieri* y *P. taurus*, con las cuales comparte similitudes en lepidosis y hábitos, siendo las tres especies de apéndices relativamente largos, cola corta, y que viven en los lugares más altos. Las especies del desierto derivadas de un progenitor como *P. coronatum* no divergen como una politomía, sino como una serie de ramas secuenciales. *Phrynosoma modestum* y *P. mcallii* no son especies hermanas. En cambio, *P. modestum* y *P. platyrhinos* son taxones hermanos compartiendo un ancestro común más reciente. *Phrynosoma mcallii* representa el taxon hermano de ambas especies. Un árbol de distancia patrística generado por computación revela que la mayoría de los miembros del grupo de la radiación del norte han sobrellevado cambio evolutivo anagenético considerable comparado con los miembros del grupo del sur, los cuales son los menos evolucionados de los ancestros comunes. Las especies del grupo del sur comprenden un conjunto relictual y la especiación dentro de éste puede haberse producido antes que ocurriera la mayor parte de la diversificación del grupo del norte.

Un estudio de los patrones de caracteres revela algunos ejemplos sorprendentes de similitud homoplástica entre algunos miembros de los dos grupos. Los caracteres convergentes envuelven: 1) la disposición espacial de los elementos nasales, maxilares, y prefrontales; 2) la posición y ángulo de entrada de las ventanillas (nostrils); 3) la extensión de sobreposición del coronoides con el dentario y surangular; 4) la formación de una barra supraorbital completa; 5) la extensión de desarrollo de los cuernos parietal y escamosal; 6) la extensión de participación de la maxila en el borde orbital; 7) el grado de expansión del ectopterygoides; 8) la orientación del supraoccipital; 9) la orientación del postorbital; 10) la longitud de los segundos ceratobranquiales; 11) el número de vértebras caudales; 12) el desarrollo y número de filas gulares agrandadas; 13) el número de filas de escamas abdominales laterales ("lateral abdominal fringe scale rows").

Se desarrolló un escenario de la historia evolutiva de *Phrynosoma* en base a los modelos paleoecológicos y paleogeográficos publicados. La evidencia fósil es fragmentaria y no provee fundamento empírico para el cladograma. El tardío *Phrynosoma holmani* del Plioceno tiene un dentario angular que es considerado una sinapomorfía para *P. cornutum* y las especies emparentadas. *Phrynosoma josecitense* del Pleistoceno, aunque no está estrechamente relacionado con *P. solare*, parece estar relacionado posiblemente con *P. coronatum* o *P. orbiculare*.

Phrynosoma y el conjunto de las lagartijas avenícolas (*Callisaurus*, *Cophosaurus*, *Holbrookia*, y *Uma*) son grupos hermanos dentro de los sceloporines. El clade de las lagartijas avenícolas y *Phrynosoma* se basa en un número de sinapomorfías, incluidos cinco caracteres osteológicos (Presch, 1969; de Queiroz, 1982) y un carácter miológico (Arnold, 1984). Cuatro características miológicas adicionales pueden compartirse entre los dos grupos (Blackburn, datos no publicados). Externamente *Phrynosoma* y el grupo de las lagartijas avenícolas tienen supralabiales oblicuos. Además, *Phrynosoma* tiene una serie de escamas mentonianas las que se alargan posteriormente y que pueden ser homólogas a una serie de escamas sublabiales que también se alargan posteriormente en las lagartijas avenícolas. *Phrynosoma* comprende un grupo morfológicamente único, notoriamente distinto de todos los otros sceloporines.

INTRODUCTION

The horned lizards (genus *Phrynosoma*) comprise a most peculiar group of morphologically specialized, largely ant-

eating sceloporine iguanids. Their general appearance is unique among iguanid lizards; the body is relatively squat and flattened, and the dorsum has enlarged spinose, or carinate scales, interspersed among much smaller scales. The head typically bears enlarged horns, and, in all species except one, the lateral abdominal area has one or two rows of enlarged fringe scales. Morphological evolution within *Phrynosoma* has involved many aspects of the external and internal morphology, but the most striking changes have occurred in the cranium and pectoral girdle. The sternum has become more expanded and distinctly pentagonal, with a wide posterior border and enlarged fontanelle. The interclavicle median process has been shortened or lost completely. The suprascapula has become a rectangular, rather than fan-shaped, structure. Evolution of the squat, depressed habitus has also involved a reduction in the number of caudal vertebrae. The cranium has widened and the snout has shortened. In most species, enlarged horns have developed on the parietal and squamosal elements, and small tubercles or horns have appeared on the dentary, prearticular, surangular, frontal, postorbital, and jugal as well. The ectopterygoids, palatines, and pterygoids have expanded, with a concomitant reduction of the suborbital fossa; the vomers have become triangular. Horned lizards have lost the lacrimal and postfrontal bones, and the epipterygoids have become reduced and attached to the prootic, or variably lost (Etheridge, 1964; Presch, 1969; Axtell, 1986).

The most recent work dealing with the phylogenetic systematics of *Phrynosoma* was that of Presch (1969). The results of his phylogenetic study largely refuted, or rendered improbable, the conclusions drawn previously by Reeve (1952). Presch also reevaluated the intergeneric relationships of the horned lizards, rejecting Etheridge's (1964) removal of the genus from the sceloporines. Presch concluded that *Phrynosoma* is a member of the sceloporines and probably the sister taxon of the sand lizard genera (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*). He cited the following synapomorphies between the two groups: 1) a shortened interclavicle median process; 2) anterolateral processes of the frontals overlapped by the nasals; 3) loss of the lacrimal; and 4) loss of the postfrontal. Presch also noted the shared absence of clavicular hooks, a symplesiomorphy, which he apparently treated as a synapomorphy in the abstract of his 1969 paper, and again in a later paper (Presch, 1970). With regard to the absence of the lacrimal, I discuss herein the possibility that it has been lost independently in *Phrynosoma* and the sand lizards. De Queiroz (1982), noting incongruities between Presch's (1970) data on scleral ossicles and the data from other workers, reexamined the scleral ossicle patterns in the sceloporines. He found high variability in ossicle pattern within genera and species and suggested that it precluded the use of much of the information for elucidating phylogenetic relationships. De Queiroz concluded, however, that all sceloporines are united by the apomorphic reduction (or loss) of ossicle 8, and furthermore, that *Phrynosoma* and the sand lizard group share the reduction (or loss) of ossicle 6.

Gorman (1973) presented karyotypic evidence consistent with the hypothesis that horned lizards are sceloporines. Data

from seven species indicated a diploid complement of 34, with 12 macrochromosomes and 22 microchromosomes. All other sceloporines, except the karyotypically variable genus *Sceloporus*, are characterized by this diploid number.

Wyles (1980) assessed the phylogenetic relationships of the sceloporine lizards in terms of morphological, immunological, and electrophoretic data. Phenograms based on Nei electrophoretic distance (D; Nei, 1972) consistently placed *Phrynosoma* within the sceloporine group and close to the sand lizard genera (see Wyles, 1980:fig. 5). The D values between *Phrynosoma* and other selected iguanid genera are as follows: *Callisaurus* (1.07), *Uma* (0.89), *Sator* (0.89), *Sceloporus* (1.21), *Urosaurus* (0.91), *Uta* (1.14), *Petrosaurus* (1.14), *Crotaphytus* (1.70), and *Dipsosaurus* (1.70). However, phenograms generated from albumin immunological data (Wyles, 1980:fig. 4) placed *Phrynosoma* farther away from the sand lizard group and as one of the earliest offshoots from the sceloporine assemblage. Wyles concluded that *Phrynosoma* and *Urosaurus* are the two oldest sceloporine genera, with an estimated time of divergence of 28–30 million years.

More recent evidence from the cloacal and hemipenial musculature of lizards (Arnold, 1984) supports the placement of *Phrynosoma* within the sceloporines and near the sand lizard assemblage. In all sceloporines examined by Arnold, including *Phrynosoma*, the *M. retractor lateralis posterior* is completely divided, a condition not observed in other iguanids. The monophyletic nature of the sceloporines, with *Phrynosoma* included, is supported by this feature. Moreover, in *Phrynosoma* as well as in *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*, the anterior fibers of the *M. retractor lateralis anterior* are reflected outwards or posteriorly just before insertion on the cloaca. This character state is not seen elsewhere in the iguanid family. Blackburn (unpubl.) has noted four additional myological features that are shared between *Phrynosoma* and the sand lizards: 1) the cranial fibers of the *M. transversus* insert along the xiphisternal rod and rib rather than in a sheet of fascia that attaches to the inner surfaces of the inscriptional ribs; 2) half or more of the fibers of the *M. costocoracoideus* insert on the sternum rather than the sternoscapular ligament; 3) the *M. obliquus internus* inserts directly on the lateral portions of the sternal inscriptional ribs or directly on the bony ribs dorsal to their curvatures rather than by tendons on the sternum and the medial portions of the sternal inscriptional ribs; and 4) the *M. omosternohyoideus pars superficialis* differentiates. In sum, *Phrynosoma* is the sister taxon of the sand lizard genera, but the morphological and immunological evidence (Presch, 1969; Wyles, 1980) would seem to indicate either a long history of separation, or rapid evolutionary divergence between the two groups.

I present here a reassessment of the phylogenetic relationships of the species of *Phrynosoma*. My interest in pursuing a reexamination of the horned lizards was prompted for the following reasons. *Phrynosoma* has remained a problematic group from a systematic standpoint. Most of the species are separated from one another by substantial morphological gaps and, therefore, the process of elucidating relationships and tracing the phylogeny is rendered difficult. On the basis

of the osteological data obtained by Presch (1969), few synapomorphies support the branching arrangement of his cladogram. Moreover, the affinities of some *Phrynosoma* species are based on the shared loss, or reduction, of skeletal elements. Phylogenetic inferences based on “loss” synapomorphies are tenuous because such “loss” character states have little information content compared with states involving the gain or elaboration of structures. The principal difficulty with “loss” character states is that most of the criteria for homology determination (Remane, 1956; Ruppert, 1982) cannot be applied in the absence of structure. In my opinion, the interrelationships among some species of *Phrynosoma* have remained ambiguous for this reason.

Second, dry skeletal preparations of *Phrynosoma ditmarsii* Stejneger and *P. taurus* Duges were not available during Presch’s study, and because radiographic techniques may yield equivocal information for some osteological features, it was deemed necessary to examine skeletal material of the two species. My interest in the group was further stimulated in 1976, when T.R. Van Devender suggested (pers. comm.) that *P. ditmarsii* was not closely related to *P. douglassii* (Bell) based on his osteological comparisons.

Finally, the need to integrate skeletal and external morphological information for comparative studies of this group of lizards appeared obvious. Presch’s conclusions were drawn entirely from osteological data, and a substantial amount of information pertaining to the external morphology of *Phrynosoma* lay unused in the literature. Consequently, my study has incorporated data from the skeletal and external morphology of the horned lizards and, due to further search, has used characters not previously evaluated in the phylogenetic systematics of the group. My paper represents a first approximation of the interspecific relationships of *Phrynosoma* based on this combined data set. A molecular study would be of value to further test the conclusions drawn herein.

MATERIALS AND METHODS

Alcohol-preserved specimens, cleared and stained skeletons, and dried skeletons, including dermestid- and hand-cleaned preparations, were examined in this study. Radiographs were not used. The cartilaginous hyoid apparatus was examined following careful dissection from alcoholic specimens. The known, extant species of *Phrynosoma* were studied, but *P. boucardii* A. Dumeril and Bocourt and *P. cerroense* Stejneger are not given much further consideration. Montanucci (1979) reviewed the external morphology and osteology of *boucardii* and concluded that it should be relegated to a subspecies of *P. orbiculare* (Linnaeus). The insular *cerroense* is closely related to *P. coronatum* (Blainville) and presents no phylogenetic problems.

The material examined is listed below. Each species of *Phrynosoma* is followed by the number of alcoholic specimens and the number of complete skeletons or skulls. *Phrynosoma asio* Cope (28, 9); *P. braconnieri* A. Dumeril and Bocourt (40, 4); *P. cornutum* (Harlan) (26, 56); *P. coronatum* (21, 27); *P. ditmarsii* (26, 4); *P. douglassii* (86, 22); *P. mcallii* (Hallowell) (17, 16); *P. modestum* Girard (26, 8); *P. orbic-*

Table 1. Variation in the angle of slant (in degrees) of the premaxilla among the species of *Phrynosoma*. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation). See text for further information.

Species	N	$\bar{X}$	S.E.	S.D.	Range
<i>P. asio</i>	7	59.0	—	—	56–62
<i>P. braconnieri</i>	3	57.0	—	—	56–58
<i>P. cornutum</i>	20	73.7	0.8	3.6	66–79
<i>P. coronatum</i>	23	65.6	1.4	6.8	53–77
<i>P. ditmarsii</i>	1	64.0	—	—	—
<i>P. douglassii</i>	14	59.7	—	—	47–70
<i>P. mcallii</i>	13	70.6	—	—	67–75
<i>P. modestum</i>	5	73.2	—	—	70–77
<i>P. orbiculare</i>	6	56.0	—	—	49–62
<i>P. platyrhinos</i>	18	72.2	0.8	3.4	66–76
<i>P. solare</i>	10	64.6	—	—	58–71
<i>P. taurus</i>	2	54.5	—	—	49–60

ulare (50, 7); *P. platyrhinos* Girard (14, 32); *P. solare* Gray (13, 17); *P. taurus* (20, 2). See Appendix for museum numbers.

My initial selection of potentially useful characters was made from the detailed systematic treatments of the genus by Reeve (1952) and Presch (1969) and subsequently enlarged following the study of specimens. Characters used in the phylogenetic analysis were those having interspecific variation, but being relatively conservative within species. The level of intraspecific character variation (racial and individual) could not be adequately ascertained in some cases due to small sample size, especially for skeletal characters. My terminology follows that used by Smith (1946), Reeve (1952), Oelrich (1956), and Presch (1969). Line illustrations of morphological features were made directly from specimens using a drawing tube mounted on a Wild M-5 dissecting microscope.

Discrimination between derived and ancestral character states was accomplished by “out-group” comparisons (see Phylogenetic Analysis) involving the other sceloporine genera and the crotaphytines. Morphological information pertaining to these external groups was obtained from the literature and from examination of specimens. The species examined are listed below; the number of alcoholic specimens and skeletons follows in parentheses. *Callisaurus draconoides* Blainville (3, 4); *Cophosaurus texanus* Troschel (4, 0); *Crotaphytus collaris* (Say) (3, 5); *Crotaphytus insularis* Van Denburgh and Slevin (1, 1); *Gambelia wislizenii* (Baird and Girard) (2, 2); *Holbrookia elegans* Bocourt (1, 0); *Holbrookia maculata* Girard (1, 0); *Petrosaurus mearnsi* (Stejneger) (6, 1); *Petrosaurus slevini* (Van Denburgh) (6, 1); *Petrosaurus thalassinus* (Cope) (6, 2); *Sator angustus* Dickerson (6, 0); *Sator grandaevus* Dickerson (6, 0); *Sceloporus graciosus* Baird and Girard (0, 2); *Sceloporus grammicus* Wiegmann (0, 3); *Sceloporus merriami* Stejneger (1, 0); *Sceloporus oc-*

cidental Baird and Girard (2, 5); *Sceloporus parvus* Smith (6, 0); *Sceloporus undulatus* (Latreille) (2, 4); *Sceloporus variabilis* Wiegmann (0, 2); *Uma notata* Baird (3, 1); *Urosaurus auriculatus* (Cope) (0, 2); *Urosaurus graciosus* Hallowell (6, 0); *Urosaurus microscutatus* (Van Denburgh) (6, 0); *Uta stansburiana* Baird and Girard (1, 6). See Appendix for museum numbers.

MORPHOLOGICAL VARIATION

Detailed descriptions of the skeletal and external morphology of *Phrynosoma* have been published in a number of papers, most notably Cope (1892, 1900), Bryant (1911), Van Denburgh (1922), Smith (1946), Reeve (1952), Savage (1958), Etheridge (1964), and Presch (1969). Accordingly, the following discussions do not provide detailed morphological descriptions, but rather focus on interspecific and intraspecific variation in morphological features that have potential value as systematic characters in this group of lizards. Character acronyms are given in parentheses for morphological features used as characters in the phylogenetic analysis. My observations and descriptions are compared with those of previous authors, and significant discrepancies are noted and discussed. I have included only a few statements pertaining to the possible functional significance of some characters in the analysis of character distribution patterns. This was done as a matter of interest, not as a methodological procedure, and did not influence the analysis itself. Little information is presented here concerning the morphology of the mandible and dentition in *Phrynosoma*. This information, as it relates to the feeding ecology of horned lizards, is being prepared for publication elsewhere.

SKELETAL MORPHOLOGY

PREMAXILLA. The angle of ascent of the premaxilla (character PMAX) from its base to the point of suture with the nasals varies within and between species of *Phrynosoma*. Presch (1969) noted the nearly vertical orientation of the premaxilla in some species (e.g., *P. platyrhinos*) and the more gradual slant of the element (ca. 50°) in others, e.g., *P. asio*. I quantified the variation by measuring the angle of repose of the premaxilla with a protractor, using the labial margin of the maxilla as a line of reference for the horizontal (Table 1, Fig. 1). The slant of the premaxilla is quite steep in *P. cornutum*, *P. mcallii*, *P. modestum*, and *P. platyrhinos*. The premaxillary spine has a more or less convex profile in *P. cornutum*, but in *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare* the premaxilla is usually flat or concave, sometimes convex near its suture with the nasals. In the latter four species, the base of the premaxilla and the maxillae are flared anteriorly to produce a rostral lip (character RLIP). The lip is reduced in *P. modestum* and absent in *P. cornutum*. Cope (1900) described *P. solare* as lacking a prominent lip border, but I found it especially pronounced (Fig. 1). In the other sceloporine genera and the crotaphytines, the premaxilla typically slants at a low angle. In *Phrynosoma*, the more steeply

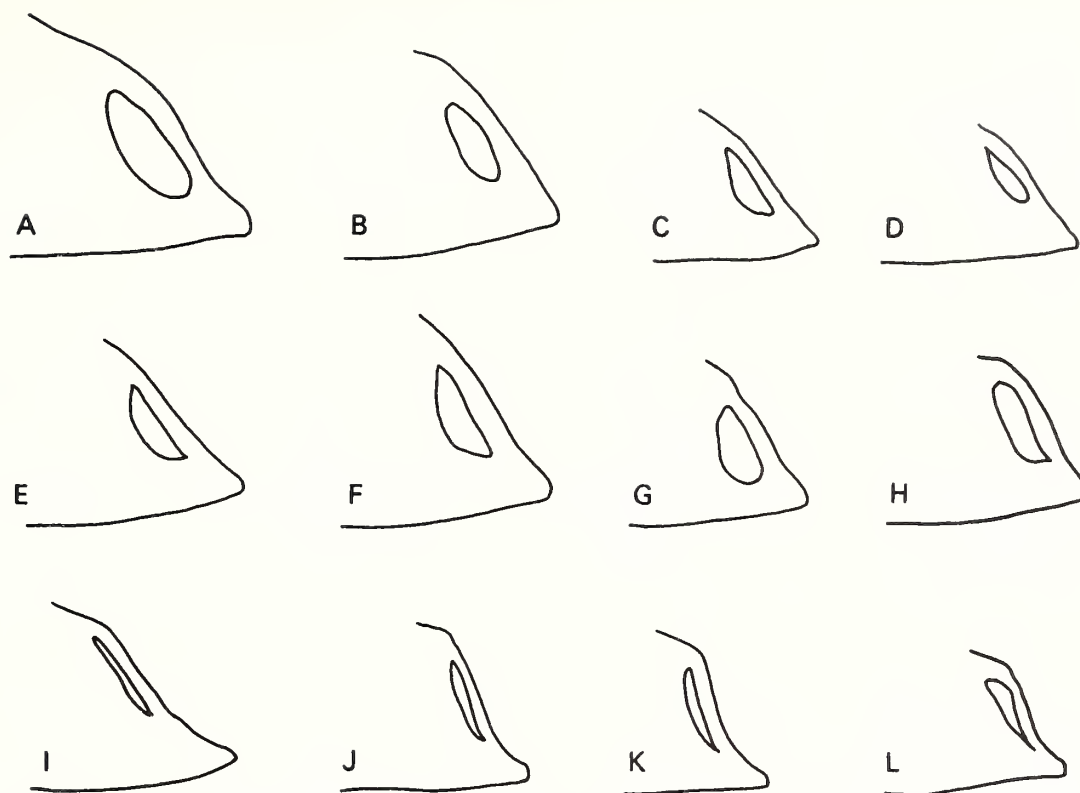


Figure 1. Representative profiles of the premaxillary area of *Phrynosoma*. Species are A, *P. asio* (AMNH 19378); B, *P. ditmarsii* (UAZ 35511); C, *P. braconieri* (AMNH 102748); D, *P. taurus* (CAS 141361); E, *P. orbiculare* (MVZ 137792); F, *P. douglassii* (AMNH 77050); G, *P. coronatum* (AMNH 77052); H, *P. cornutum* (AMNH 90804); I, *P. solare* (AMNH 1285); J, *P. mcallii* (AMNH 77045); K, *P. platyrhinos* (AMNH 68612); L, *P. modestum* (AMNH 74499).

oriented element and presence of a rostral lip are considered derived states.

NASAL. The posterior process of the nasal is flat, but the anterior process forms an acute angle (character RSFA) to meet the premaxilla in *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*. Anteriorly, the prefrontals may participate with the nasals in forming this abrupt angle (the rostrofrontal angle of Reeve, 1952, and the interpreorbital angle of Cope, 1900). The acute angle is formed because the nasals suture anteriorly with the steeply ascending spine of the premaxilla, and posteriorly with the frontal which is flattened, almost horizontally oriented. The premaxilla ascends less steeply in *P. solare* than in the other four species (Table 1), and the angle in the nasals is less abrupt and more rounded. In both *P. cornutum* and *P. solare*, the angle in the prefrontals also tends to be rounded. In the remaining species within the genus, the nasals are flat, or produce only a slight angle; hence the skull has a gradually sloping profile. A gradually sloping profile is also seen in the other sceloporine genera and the crotophytines.

MAXILLA. The nasal process of the maxilla reaches the nasal bones (character NAMX) in *P. asio*, *P. coronatum*, *P. ditmarsii*, *P. douglassii*, and *P. orbiculare*. The two elements are separated by the prefrontal in *P. braconieri*, *P. cornutum*,

P. mcallii, *P. modestum*, *P. platyrhinos*, *P. solare*, and *P. taurus* (Fig. 2). My observations agree with those of Presch (1969), but he had no information for *P. ditmarsii* and *P. taurus*. Etheridge (1964:621) stated, apparently in error, that the maxillae and nasals are in contact in *P. mcallii*. The nasal process of the maxilla reaches the nasal bones in the other sceloporine genera and in the crotophytine lizards. Contact between the maxillae and nasals is therefore regarded as the ancestral condition.

The maxilla may form, to a greater or lesser degree, part of the anteroventral margin of the orbit in *Phrynosoma*. In some specimens, the anterior process of the jugal extends forward to meet the prefrontal, excluding the maxilla entirely from the orbital border. Presch (1969) noted that the element is excluded from the orbital margin in *P. orbiculare*. However, I found it to vary in *P. orbiculare*, as well as in the other species (Table 2). The jugal excludes the maxilla (zero percent values in Table 2) in some specimens of *P. asio*, *P. coronatum*, *P. ditmarsii*, *P. douglassii*, *P. mcallii*, *P. orbiculare*, and *P. platyrhinos*. In the other sceloporine genera and the crotophytines, the maxilla is excluded from the orbital margin. *Phrynosoma* species with the lowest mean values are *P. asio*, *P. ditmarsii*, *P. mcallii*, and *P. orbiculare*, and, hence, are most similar to the ancestral condition. *Phrynosoma cor-*

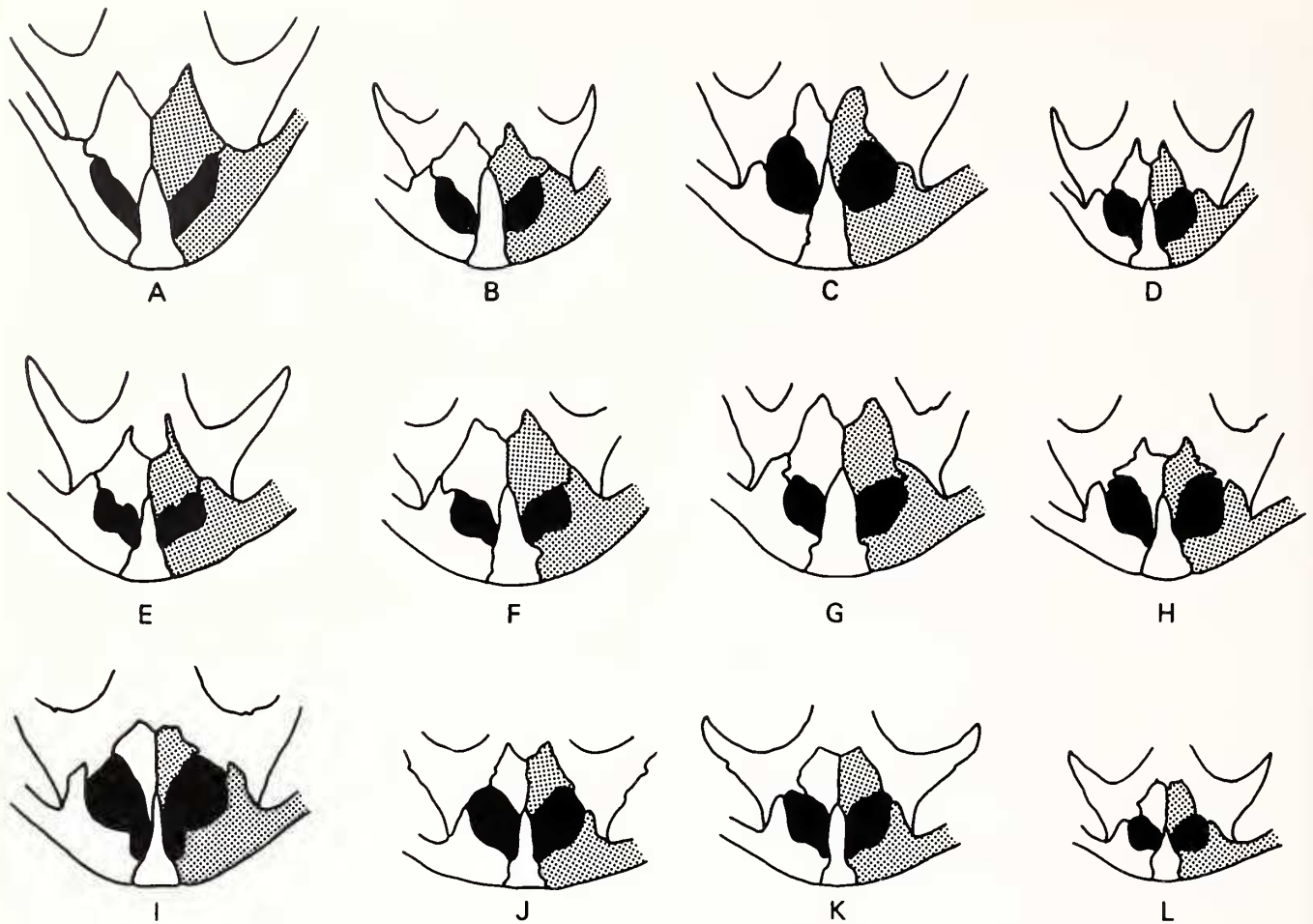


Figure 2. Variation in the arrangement of the nasal, maxilla (both stippled), and prefrontal among the species of *Phrynosoma*. Species are A, *P. asio* (AMNH 72636); B, *P. ditmarsii* (UAZ 35511); C, *P. taurus* (CAS 141361); D, *P. braconnieri* (UTA 10281); E, *P. orbiculare* (MVZ 137792); F, *P. douglassii* (KU 13943); G, *P. coronatum* (CAS 58152); H, *P. cornutum* (AMNH 15403); I, *P. solare* (AMNH 1285); J, *P. mcallii* (AMNH 77042); K, *P. platyrhinos* (AMNH 68612); L, *P. modestum* (AMNH 1327).

nutum and *P. modestum* are considered most derived for this feature.

LACRIMAL. The presence of a small lacrimal in some species of *Phrynosoma*, e.g., *P. cornutum*, *P. coronatum*, and *P. douglassii*, was reported by Cope (1900) and Bryant (1911). However, Jollie (1960), Etheridge (1964), and Presch (1969) reported that it was absent in the genus. According to Presch, the presence of a lacrimal in *Phrynosoma* was mentioned by Reeve (1952); however, I cannot find any reference to it. None of the specimens of *Phrynosoma* I have examined has a lacrimal, although in five specimens of *Phrynosoma asio* (AMNH 74838, 19378; FMNH 31315; MVZ 137771, 137776) there is a downward projecting spur from the prefrontal which could represent a vestige of the lacrimal. Absence of the lacrimal has been explained as possibly the result of loss rather than fusion (Jollie, 1960). However, if my interpretation is correct, the lacrimal may have fused with the prefrontal in *Phrynosoma*. The lacrimal is present in the crotaphytines and the sceloporine genera *Petrosaurus*, *Sator*, *Sceloporus*, *Urosaurus*, and *Uta*, but absent in *Callisaurus*, *Holbrookia*, and *Uma* (Presch, 1969). According to Zalusky

(1976), however, the lacrimal is present in *Uma* (based on cleared and stained specimens), but receded within the orbital margin and lost to view externally. A similar fate has been observed in the Gekkonidae (Camp, 1923), but for an alternative explanation in *Coleonyx*, see Kluge (1975). Loss of the lacrimal has also been noted in at least some representatives of the following lacertilian families: Scincidae, Feyliniidae (=Scincidae), Gerrhosauridae (=Cordylidae), Lacertidae, Zonuridae (=Cordylidae), and Xantusiidae (Camp, 1923). Moreover, Siebenrock (in Camp, op. cit.) noted that the lacrimal is small or lost in numerous representatives of Agamidae. Zalusky's report (1976) of a lacrimal in *Uma* needs to be confirmed. If correct, it suggests the possibility of independent loss of the bone in *Phrynosoma* on the one hand and some of the sand lizards on the other. Alternatively, the presence of the element in *Uma* could be regarded as a neomorph. The absence of the lacrimal in *Phrynosoma* is tentatively considered a derived state.

ECTOPTYERYGOID. The anterior expansion of the ectopterygoid (character ECTO) varies among the species of *Phrynosoma*. Presch (1969) noted anterior expansion of the

element in all species of *Phrynosoma* except *P. orbiculare* which has little or no expansion. In the remaining species, as the element becomes shortened anterior to posterior, there is increased expansion. In the other sceloporine genera and crotaphytines, the ectopterygoid is not expanded. The shape and orientation of the element in *P. orbiculare* are similar to those noted in other sceloporines. The derived condition in *Phrynosoma* is represented by an expanded and shortened element.

JUGAL. The temporal process of the jugal is expanded (character JUSH) in *Phrynosoma* (Presch, 1969), but there is considerable variation in the degree of expansion and general shape of the element among the species (Fig. 3). The jugal is relatively narrow at its posterior end in *P. asio*, but less so in *P. ditmarsii*. In the other species, the element is more expanded. In *P. braconneri* and *P. taurus*, the bone is triangular, greatly expanded, with a nearly flat posterior border (character JUSA). In *P. douglassii* and *P. orbiculare* the border slopes posteriorly. In *P. cornutum*, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*, the posterior border slants anteriorly. In the other sceloporine genera and the crotaphytines, the jugal is long and slender.

Table 2. Variation in the length of the maxilla contacting the orbital margin, expressed as a percentage of the total length of the maxilla. Zero values in the columns for mean and range indicate that the maxilla is completely excluded from the orbital margin by the anterior jugal process. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation).

Species	N	$\bar{X}$	S.E.	S.D.	Range
<i>P. asio</i>	9	2.2	—	—	0–8.7
<i>P. braconneri</i>	3	7.5	—	—	6.3–9.3
<i>P. cornutum</i>	33	21.5	1.1	6.2	11.3–35.1
<i>P. coronatum</i>	33	7.4	1.2	6.7	0–23.6
<i>P. ditmarsii</i>	1	0	—	—	—
<i>P. douglassii</i>	23	6.7	1.4	6.8	0–21.4
<i>P. mcallii</i>	17	0.7	0.3	1.4	0–4.4
<i>P. modestum</i>	6	18.1	—	—	11.1–22.2
<i>P. orbiculare</i>	10	2.8	—	—	0–7.9
<i>P. platyrhinos</i>	35	9.9	0.9	5.6	0–25.0
<i>P. solare</i>	18	11.4	0.6	2.5	7.1–17.0
<i>P. taurus</i>	2	9.3	—	—	5.3–13.2

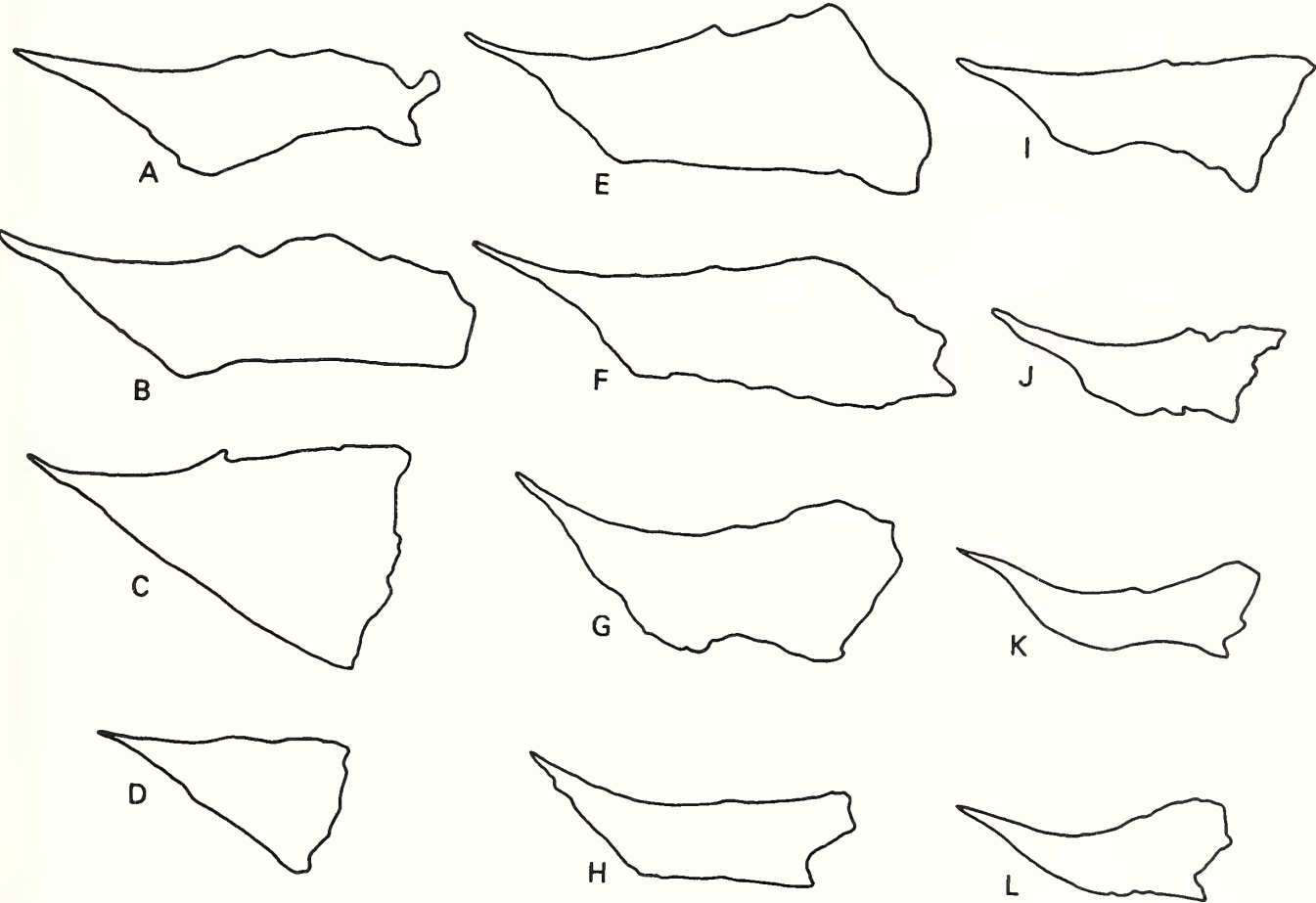


Figure 3. Variation in the shape of the jugal among the species of *Phrynosoma*. Species are A, *P. asio* (MVZ 137771); B, *P. ditmarsii* (UAZ 35511); C, *P. taurus* (UTA 17129); D, *P. braconneri* (UTA 10281); E, *P. orbiculare* (MVZ 137792); F, *P. douglassii* (MVZ 77046); G, *P. coronatum* (MVZ 272); H, *P. cornutum* (MVZ 78385); I, *P. solare* (MVZ 79602); J, *P. mcallii* (MCZ 44822); K, *P. platyrhinos* (UMMZ 149123); L, *P. modestum* (UMMZ 149121).

The surface of the jugal (character JUSU) is quite smooth with a weak, convex ridge in *Phrynosoma asio*. In *P. braconneri* the surface is slightly rugose with one to three weak tuberosities. The surface is more strongly rugose in *P. taurus*. There is a series of several low tuberosities with or without a distinct process at the posterior end of the bone in *P. douglassii*. The tuberosities are prominent in some specimens, especially in *P. d. hernandesi*. In *P. orbiculare*, the jugal usually bears one or two low tuberosities, and a more pronounced one at its posterior edge. In *P. ditmarsii* there is a linear series of three to six low, but peaked, tuberosities along a convex ridge on the bone. The jugal has two to three horn-like processes in *P. coronatum* and *P. solare*, and three to five processes in *P. cornutum*, *P. modestum*, *P. mcallii*, and *P. platyrhinos*. The element is essentially smooth in other groups of sceloporines and the crotophytines.

FRONTAL. The frontal is T-shaped and forms the medial and posterior borders of the orbits. The dorsal surface of the frontal is remarkably smooth in *Phrynosoma asio*, but is ornamented in the other species. In *P. coronatum*, the medial border area may be smooth or rugose, and there may be one or several low, rounded, or peaked tubercles along the posterior orbital borders. In *P. braconneri* and *P. taurus*, a series of rounded, slightly peaked tubercles extends from the posterior orbital border to the posterior half of the medial border. In *P. ditmarsii*, the medial border is rugose, and there are three to four peaked tubercles along the posterior orbital border. In *P. douglassii*, the anterior half of the medial border area is rugose, changing to low, rounded, rugose tuberosities posteriorly, and in some specimens, becoming peaked tubercles. In *P. orbiculare*, weak rugosities or low tubercles occur along the medial border area, becoming somewhat peaked and enlarged along the posterior orbital border. In *P. mcallii*, *P. modestum*, and *P. platyrhinos*, the surface of the frontal has low, rounded, rugose tuberosities, which become slightly peaked posteriorly. The ornamentation extends nearly the entire length of the frontal in *P. mcallii*, but is limited to the posterior half of the element in *P. modestum* and *P. platyrhinos*. In *P. solare*, there is a series of low, peaked tubercles which become prominent near the superciliary spine. In *P. cornutum*, the frontal has peaked tubercles which become enlarged processes along the posterior orbital border. The frontal is relatively smooth in the majority of the other sceloporine genera and the crotophytines.

PARIETAL. The dorsal surface of the parietal is relatively smooth, with slight, rounded elevations in *Phrynosoma asio*. In the other species, the parietal surface is ornamented. In *Phrynosoma taurus* the surface is rugose, with low tubercles and ridges that appear to radiate from the center of the element. In *P. ditmarsii* the parietal surface is less rugose, with two low tubercles. The parietal surface may have two or more low tubercles and may or may not be slightly rugose in *P. douglassii*. The tubercles are slightly more conical and pointed in *P. braconneri* and *P. orbiculare*, and appear more elongate and spine-like in some *P. coronatum*, *P. cornutum*, and *P. solare*. The parietal surface has low, rugose tuberosities in *P. mcallii*, *P. modestum*, and *P. platyrhinos*. The parietal is without surface ornamentation in the other sceloporine genera and the crotophytine genera.

In *Phrynosoma*, low tuberosities, and conical and spine-like tubercles represent progressively derived features.

The posterior margin of the parietal (character PANO) forms a deep, narrow notch in *Phrynosoma ditmarsii*. In the other species of *Phrynosoma* such an indentation is lacking; its unique presence in *P. ditmarsii* is a derived condition.

Phrynosoma solare is the only member of the genus with four parietal horns; this unique feature probably represents a derived character state. All other horned lizards have two horns, and in some species the horns are greatly reduced. The origin of the extra pair of parietal horns in *P. solare* is open to speculation. Most *Phrynosoma* species have several enlarged scales at the base of the parietal horns. One of the scales located dorsolaterally on the base (character PARS) is enlarged and projecting in *P. modestum*, *P. mcallii*, and *P. platyrhinos*, especially so in the latter two species. I suggest that the additional parietal horn arose from this bony projection. Alternatively, there is an enlarged scale (which is developed as a projection only in some *P. coronatum*) medial to the base of the last squamosal horn. This scale would seem less probable as the point of origin because it is located on the squamosal, not the parietal bone.

There is considerable variation in the length of the parietal horns among the species of *Phrynosoma*. Also, there appears to be geographic variation in horn length in several species, e.g., *Phrynosoma douglassii* and *P. coronatum*, which have extensive latitudinal distributions. The parietal horns were measured and the length was expressed as a percentage of the skull length in each species. The range in variation of parietal horn length was used to establish categories, more or less arbitrarily. The categories, range of variation (in parentheses), and assigned species, are as follows: 1) very short (6.9–11.2%), *Phrynosoma ditmarsii*; 2) short (12.1–20.1%), *P. douglassii*, *P. taurus*; 3) moderate (17.9–29.7%), *P. asio*, *P. braconneri*, *P. modestum*, *P. orbiculare*; 4) moderately long (33.7–41.9%), *P. platyrhinos*; 5) long (37.8–60.2%), *P. cornutum*, *P. coronatum*, *P. solare*; and 6) very long (60.8–66.2%), *P. mcallii*.

SUPRAOCCIPITAL. In *Phrynosoma*, the dorsal border of the supraoccipital bears a stout midsagittal process, and an anterolateral process on each side upon which the posterior border of the parietal rests (Presch, 1969). This tripartite contact (character SPOP) is found in all species of horned lizards except *Phrynosoma asio*, in which the entire dorsal edge of the supraoccipital contacts the parietal (Fig. 4). Some interspecific variation is present in the tripartite joint in terms of the size of the foramina produced between the processes. In *Phrynosoma mcallii*, more of the dorsal edge of the supraoccipital nearly reaches the parietal so that the foramina are reduced to slit-like apertures. Thus, the condition in *P. mcallii* approaches that observed in *P. asio*. In the other sceloporine genera, there are also three points of connection between the two elements. The amount of direct bony connection appears to vary ontogenetically and interspecifically (K. de Queiroz, pers. comm.). Compared with the tripartite joint in *Phrynosoma*, the connections observed in other sceloporines are weaker and less buttressed.

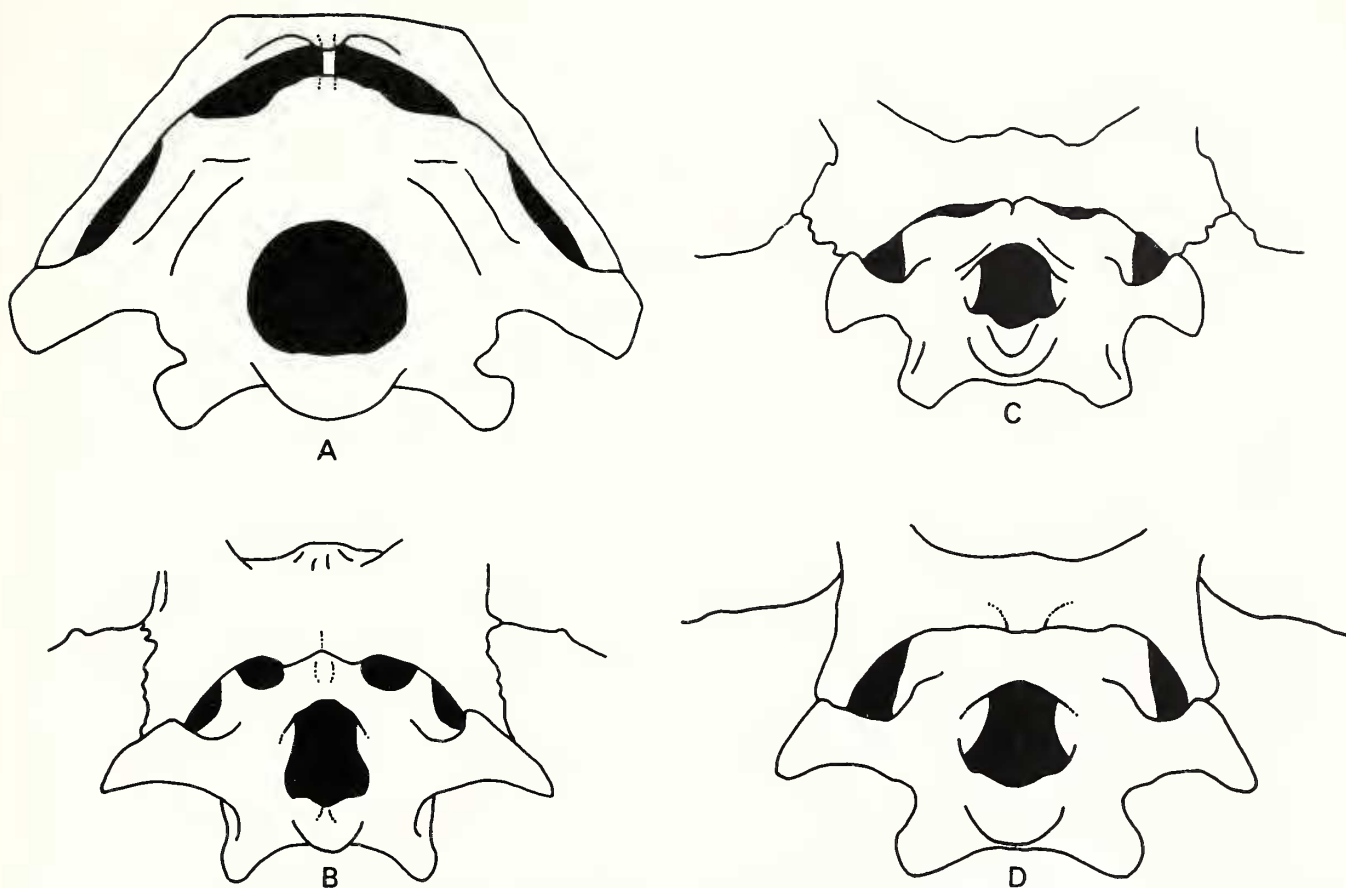


Figure 4. Posterior aspect of the skull of a representative sceloporine, A, *Urosaurus auriculatus* (LACM 132547), and three species of *Phrynosoma*: B, *P. orbiculare* (MCZ 11313); C, *P. mcallii* (MCZ 44822); and D, *P. asio* (AMNH 72636), showing variation in the joint between the supraoccipital and parietal. In *Urosaurus*, the stalk-like processus ascendens attaches under the posterior margin of the parietal.

The single midsagittal connection is by way of the processus ascendens, a slender, stalk-like, calcified element. In *Phrynosoma*, the processus ascendens is usually enclosed within the stout, median dorsal process of the supraoccipital (Presch, 1969). The complete contact between the two elements, which among horned lizards is unique to *Phrynosoma asio*, is considered a derived character state, relative to the more prevalent tripartite condition.

In *Phrynosoma*, there is variation in the angle of inclination of the supraoccipital from the edge of the foramen magnum to the median connection with the parietal. The supraoccipital extends nearly vertically to reach the parietal in *Phrynosoma braconneri*, *P. mcallii*, *P. modestum*, *P. orbiculare*, and *P. platyrhinos*. The element is nearly vertical above the foramen magnum, and then arches posteriorly to contact the parietal in *P. cornutum* and *P. solare*, but in *P. taurus* it immediately arches posteriorly. In *P. coronatum* and *P. douglassii*, orientation of the supraoccipital is vertical in some specimens, but extends anteriorly at a slight angle in others. The anterior slant is somewhat more pronounced in *P. asio* and *P. ditmarsii*. In other sceloporine genera, the supraoccipital is relatively large, and extends anteriorly to reach the

parietal bone. Hence, the condition seen in *P. asio* and *P. ditmarsii* vaguely resembles that observed in other sceloporines.

SUPRAORBITAL BAR. *Phrynosoma* is characterized by a posteriorly directed prefrontal process and an anteriorly directed frontal process; the two processes may closely approach each other, or meet to produce a complete supraorbital bar or arch (Etheridge, 1964; Presch, 1969). A complete supraorbital bar (character SBAR) is present in *Phrynosoma cornutum*, *P. mcallii*, *P. solare*, and *P. taurus*. The arch is narrowly incomplete in *P. asio*, but more widely interrupted in *P. braconneri*, *P. coronatum*, *P. ditmarsii*, *P. douglassii*, *P. modestum*, *P. orbiculare*, and *P. platyrhinos* (Table 3, Fig. 5). In species with a complete arch, the condition develops in postembryonic ontogeny, and the location of the suture between the prefrontal and frontal processes varies somewhat. It was calculated as a percentage value (distance A divided by distance B $\times$ 100; Fig. 5J). The mean and range of values obtained are: *Phrynosoma cornutum* (75.3%, 54.3–84.0%); *P. mcallii* (65.3%, 60.1–69.5%); *P. solare* (74.5%, 69.3–78.3%); and *P. taurus* (65.1%, no range). Other sceloporine genera and the crotophytines lack prefrontal and frontal

Table 3. Variation in the distance separating the ends of the prefrontal and frontal processes, expressed as a percentage of the orbital distance. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation). Zero values indicate a complete supraorbital bar.

Species	N	$\bar{X}$	S.E.	S.D.	Range
<i>P. asio</i>	7	5.4	—	—	0–14.5
<i>P. braconneri</i>	3	17.9	—	—	8.9–25.1
<i>P. cornutum</i>	11	0	—	—	—
<i>P. coronatum</i>	22	18.5	1.6	7.7	7.9–38.1
<i>P. ditmarsii</i>	1	20.4	—	—	—
<i>P. douglassii</i>	13	29.3	—	—	11.7–46.1
<i>P. mcallii</i>	7	0	—	—	—
<i>P. modestum</i>	5	47.2	—	—	41.0–56.6
<i>P. orbiculare</i>	5	24.5	—	—	8.7–43.6
<i>P. platyrhinos</i>	17	29.2	1.4	5.6	15.7–37.0
<i>P. solare</i>	7	0	—	—	—
<i>P. taurus</i>	2	0	—	—	—

processes. Hence, *Phrynosoma* species with a wide gap between the processes are close to the ancestral condition, whereas narrowly interrupted and complete bony arches represent progressively derived character states.

POSTORBITAL. The postorbital bone forms a major portion of the posterior border of the orbit. The dorsal process of the postorbital is sutured with the posterolateral corner of the frontal and the anterolateral corner of the parietal; the ventral process is joined with the jugal and squamosal (Presch, 1969). In *Phrynosoma asio*, *P. braconneri*, *P. cornutum*, *P. ditmarsii*, and *P. taurus*, the postorbital is oriented vertically (character POST) and curves outward gradually and to a limited extent. In *Phrynosoma orbiculare*, *P. douglassii*, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*, the postorbital curves outward more rapidly and to a greater degree (Fig. 6). In the latter group of species, the skull is relatively more depressed and flaring, which is possibly an adaptation for more efficient burrowing. In the crotophytines and the sceloporines, including the sand lizards, the postorbital slants outward to a lesser extent than in *Phrynosoma*. The element has little or no concave curvature, but instead is usually flat or somewhat convex.

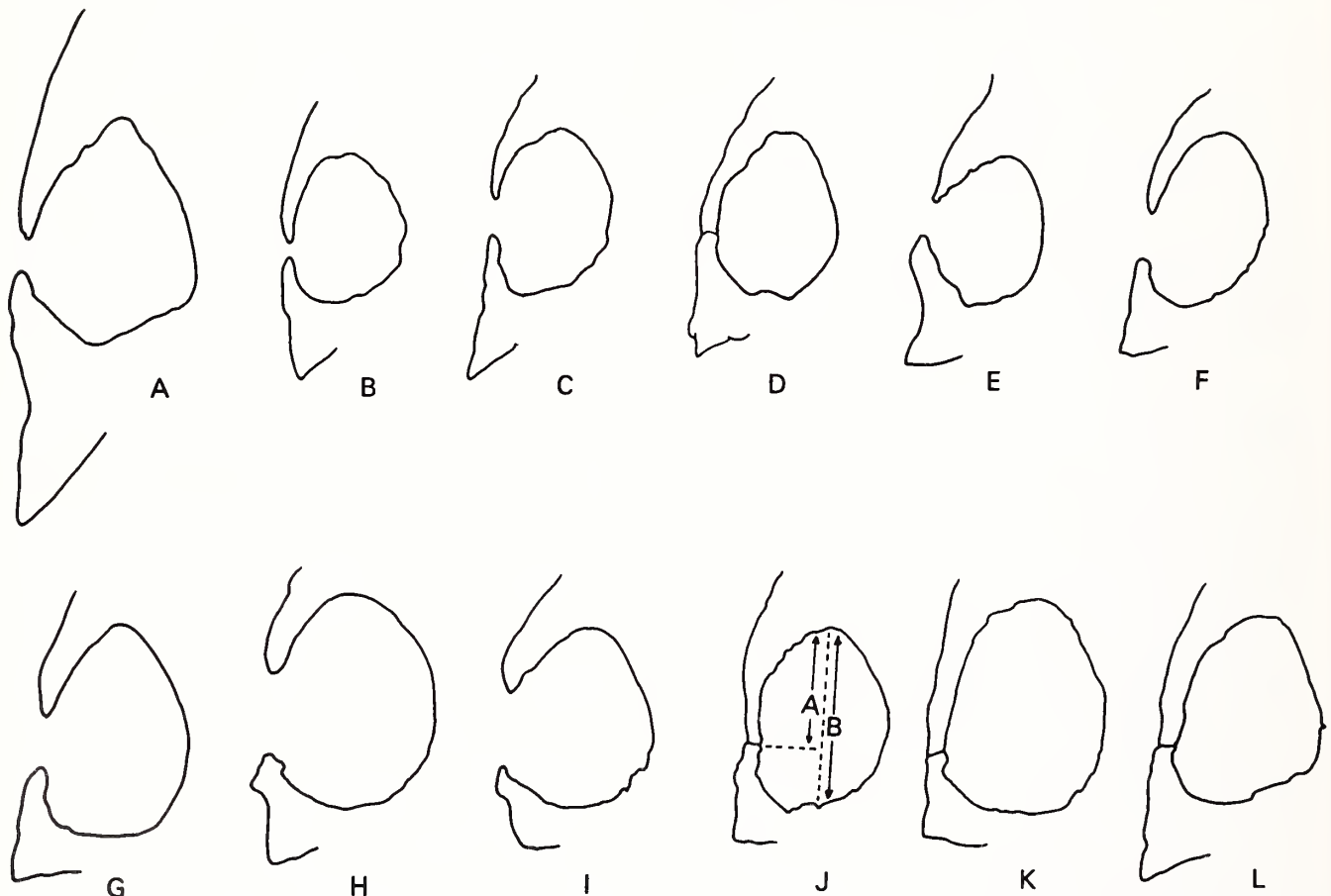


Figure 5. Variation among the species of *Phrynosoma* in the extent of closure of the prefrontal and frontal processes to form a supraorbital bar or arch. The species (in dorsal view) are A, *P. asio* (AMNH 74838); B, *P. braconneri* (AMNH 102748); C, *P. ditmarsii* (UAZ 35511); D, *P. taurus* (UTA 17129); E, *P. orbiculare* (AMNH 15423); F, *P. douglassii* (CAS 34706); G, *P. coronatum* (USNM 220242); H, *P. platyrhinos* (AMNH 77039); I, *P. modestum* (AMNH 74597); J, *P. mcallii* (MCZ 44822); K, *P. solare* (AMNH 2579); L, *P. cornutum* (MCZ 169686). J illustrates how the position of the suture between the two processes was calculated. See text for explanation.

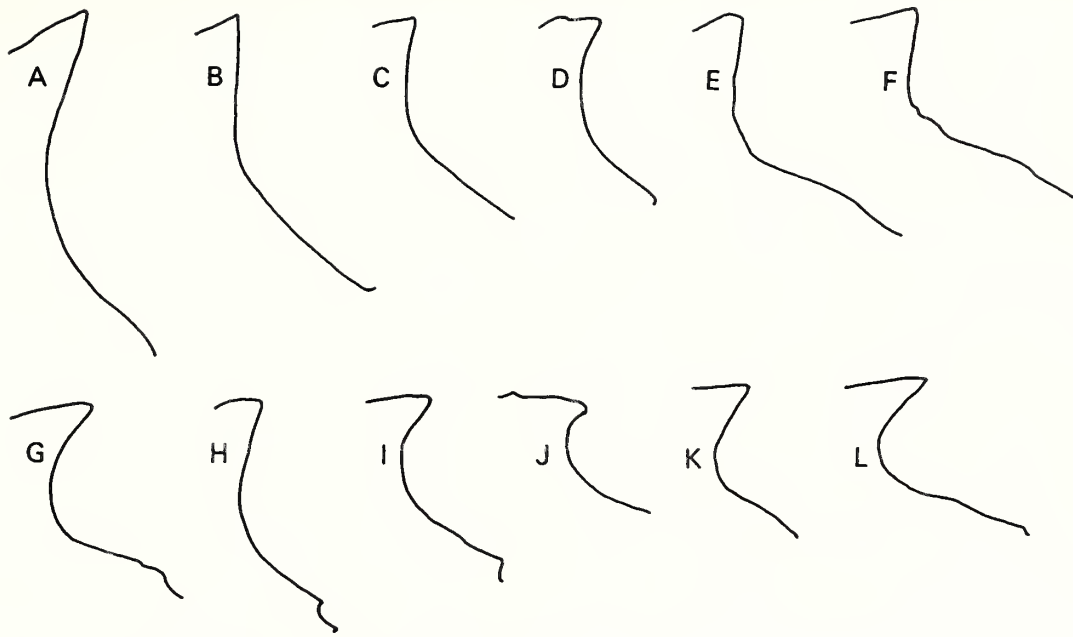


Figure 6. Posterior aspect of the right side of the skulls of *Phrynosoma*, showing variation in the orientation and slope of the postorbital. The species are A, *P. asio* (MVZ 137771); B, *P. ditmarsii* (UAZ 35511); C, *P. taurus* (UTA 17129); D, *P. braconneri* (UTA 10281); E, *P. orbiculare* (MVZ 137792); F, *P. douglassii* (MVZ 77046); G, *P. coronatum* (MVZ 272); H, *P. cornutum* (MVZ 78385); I, *P. mcallii* (MCZ 44822); J, *P. modestum* (MCZ 169857); K, *P. platyrhinos* (UMMZ 149123); L, *P. solare* (MVZ 79602).

The outer surface of the postorbital may be smooth or ornamented with small bony processes. The surface is smooth in *Phrynosoma asio*. Presch (1969) listed *P. douglassii* and *P. solare* also as having a smooth postorbital surface. However, I have noted one low tuberosity on the postorbital in some *P. douglassii*, while in the majority of *P. solare*, one or two processes are present. The remaining species, i.e., *P. braconneri*, *P. cornutum*, *P. coronatum*, *P. ditmarsii*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, and *P. taurus* have a rugose surface or one or more bony processes.

SUPRATEMPORAL FOSSA. In *Phrynosoma mcallii*, the supratemporal fossa (character SUFO) is absent in old adults, being occluded ontogenetically by bone extending inward from the parietal, squamosal, and postorbital (Norris and Lowe, 1951). The fossa is present in all other *Phrynosoma*, as well as in the other sceloporine and crotaphytine genera. Occlusion of the supratemporal fossa is a derived character state.

SQUAMOSAL. In *Phrynosoma*, the squamosal bears a variable number of horns which in most species increase in size from anterior to posterior. *Phrynosoma asio* has two horns. *Phrynosoma braconneri* typically has three horns, but in one specimen there are two additional small projections on the right side and one on the left. There are three squamosal horns in *P. cornutum*, *P. mcallii*, *P. modestum*, *P. orbiculare*, and *P. platyrhinos*. Presch (1969), however, noted four horns in *P. modestum*. The number of horns varies from two to three in *P. coronatum* and *P. douglassii*. In the latter species, there may be one or two smaller projections situated

above the normal row of horns. In *P. ditmarsii* there are three horns, with two additional, smaller projections situated between and slightly above the others. *Phrynosoma solare* has four horns. *Phrynosoma taurus* has a single large squamosal horn, flanked by two smaller spurs; additionally, there are two rugose projections on the dorsal base of the large horn. Squamosal horns are unique to the genus *Phrynosoma*, being absent in other sceloporines and crotaphytines. The ancestral condition may have been two squamosal horns. The single, greatly enlarged horn in *P. taurus* is a specialization, apparently derived from a three-horned squamosal, and involving elongation of the element and enlargement of the middle horn. *Phrynosoma taurus* is the only species in the genus having a greatly elongated squamosal bone (character SQSH). In the other horned lizard species, the squamosal forms, more or less, a rounded arch.

MANDIBLE SHAPE. The mandible is robust and has enormous vertical expansion (character MAND) in *Phrynosoma ditmarsii*, but the remaining species have no such expansion. The unique, apparently derived morphology of the lower jaw in *P. ditmarsii* is possibly an adaptation for masticating large, chitinous arthropods.

CORONOID. Presch (1969) noted that the coronoid may overlap the dentary and the surangular bones. He found overlap to be present in *P. asio*, *P. cornutum*, *P. coronatum*, *P. douglassii*, and *P. orbiculare*. Reduced overlap was noted in *P. platyrhinos* and *P. modestum*, whereas no overlap was seen in *P. braconneri*, *P. mcallii*, and *P. solare*. Additionally, I have noted overlap in *P. ditmarsii*, and reduced overlap in

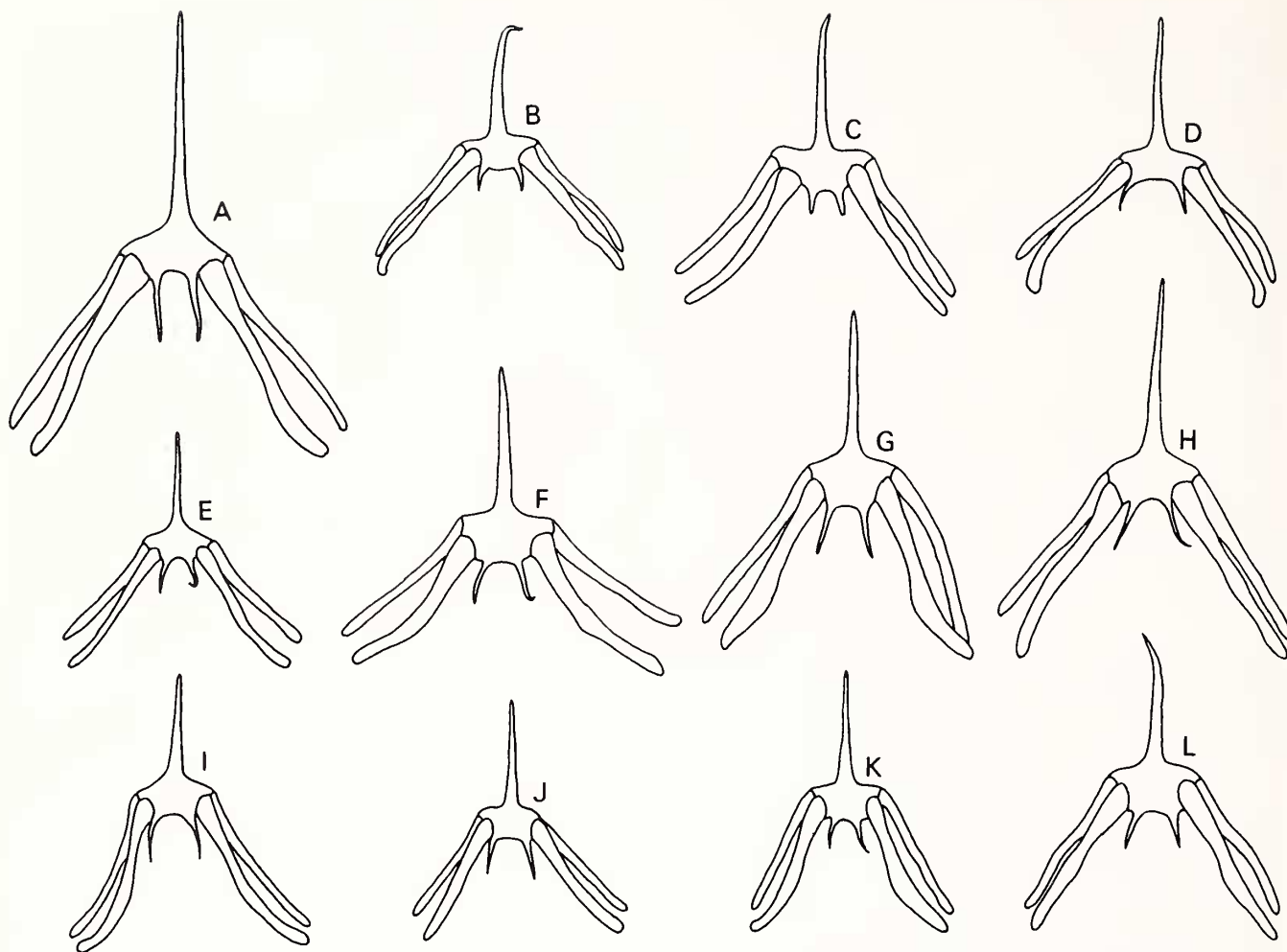


Figure 7. The hyoid apparatus in *Phrynosoma*, showing variation in the length of the second ceratobranchials. The species are **A**, *P. asio* (RRM 1754); **B**, *P. braconnieri* (UTA 4840); **C**, *P. ditmarsii* (UAZ 35511); **D**, *P. taurus* (UTA 4841); **E**, *P. orbiculare* (RRM 2378); **F**, *P. douglassii* (RRM 2389); **G**, *P. coronatum* (RRM 2395); **H**, *P. cornutum* (RRM 2094); **I**, *P. mcallii* (RRM 2397); **J**, *P. modestum* (RRM 2396); **K**, *P. platyrhinos* (RRM 2394); **L**, *P. solare* (RRM 2405).

P. taurus. Presch (1969) noted varying overlap between the elements in other sceloporines.

DENTARY. The lateral surface of the dentary (character DENS) is rounded and smooth in *Phrynosoma asio*, *P. braconnieri*, *P. coronatum*, *P. ditmarsii*, *P. douglassii*, *P. orbiculare*, and *P. taurus*. The dentary is more angular and has protuberances or horns in *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*. Presch (1969) listed, apparently in error, *P. modestum* as one of the species having a smooth dentary. He also described the dentary surface as being rugose in *P. ditmarsii*. My impression is that the lateral surface of the element is rather smooth in *P. ditmarsii*. Also, the dentary is expanded and somewhat concave posteriorly, and its lower posterior margin may bear one of several flattened, ventrally directed projections, the remainder being found on the surangular. Other sceloporine genera and the crotophytine lizards have a smooth, more or less rounded dentary surface.

SURANGULAR. The lateral surface of the surangular (character SURA) is smooth and more or less convexly rounded in *Phrynosoma coronatum*, *P. douglassii*, and *P. orbiculare*. The surangular is horizontally expanded with a prominent angular edge in *P. asio*, *P. braconnieri*, and *P. taurus*. The edge has an upturned lip in *P. braconnieri*. In *P. ditmarsii* the surangular has horns situated nearly ventrally that project at a downward angle. The outer face of the surangular bears laterally directed horns in *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*. The laterally directed horns on the surangular and dentary provide bony support for the enlarged chinshields which, so strengthened, might be more effective defensive structures, or possibly function more efficiently in burrowing. Although *P. coronatum* has enlarged chinshields, the bony supports are lacking.

ANGULAR. The angular (character ANGU) is absent in *Phrynosoma mcallii* and most specimens of *P. modestum*.

(Presch, 1969). The bone is present in the remaining species of *Phrynosoma* and in other sceloporine genera (Etheridge, 1964) and the crotaphytines. Its absence is considered a derived character state.

SPLENIAL. The splenial (character SPLN) is present in all species of *Phrynosoma* except *P. mcallii* (Presch, 1969). The element is present and well developed in the other sceloporine genera and in the crotaphytines. Loss of the splenial represents a derived condition.

HYOID. The hyoid apparatus of *Phrynosoma* varies primarily in the extent of development of the second ceratobranchials. Presch (1969) concluded that these cartilaginous processes are absent in *P. braconneri*, *P. mcallii*, and *P. solare*, present in *P. asio*, and present, but reduced, in the remaining species. In my study, the hyoid was examined in alcoholic specimens, and the entire apparatus was teased from the surrounding musculature in a water-filled petri dish. The second ceratobranchials were found in all species of *Phrynosoma* (Fig. 7). Undoubtedly, these delicate cartilaginous structures are easily lost in dried skeletal preparations. The processes are longest in *P. asio* and shortest in *P. braconneri* and *P. taurus*. Proportional values (based on length of process divided by width of hyoid body between the processes) were calculated from one specimen each as follows: *Phrynosoma asio* (2.62), *P. coronatum* (2.14), *P. orbiculare* (2.00), *P. platyrhinos* (2.00), *P. cornutum* (1.87), *P. douglassii* (1.85), *P. ditmarsii* (1.40), *P. solare* (1.37), *P. modestum* (1.37), *P. mcallii* (1.30), *P. braconneri* (1.00), and *P. taurus* (0.83). In the other sceloporines, the second ceratobranchials are long (Presch, 1969).

SUPRACORACOID FORAMEN. The supracoracoid foramen is small, and is situated anterior to the glenoid fossa in *Phrynosoma*. The foramen is present in all species of horned lizards except *P. cornutum* and *P. modestum* in which it may have become incorporated with the primary coracoid fenestra (Presch, 1969; for terminology see Etheridge, 1964:fig. 3). A small supracoracoid foramen is present in all other sceloporines (Etheridge, 1964; Presch, 1969), and therefore its absence in two species of *Phrynosoma* is considered a derived condition.

INTERCLAVICLE. The interclavicle is a median element attached to the anterior margin of the sternum, having a pair of lateral processes and, in most *Phrynosoma*, a median process (character ICMP). There is variation in the shape and orientation of the lateral processes, but apparently the variation has little systematic value. The length of the median process varies within and between species (Table 4, Fig. 8). The amount of variation within some species is considerable; see in Figure 8, for example, *P. cornutum* (nos. 5–8), *P. douglassii* (nos. 15–18), and *P. orbiculare* (nos. 22–23). This variation, at least in *P. cornutum* and *P. douglassii*, does not appear to be geographically correlated. Presch (1969) indicated that the median process is absent in *P. asio*, *P. modestum*, and *P. platyrhinos*. In my study, all three species were found to have the median process. In *Phrynosoma asio*, the process has a unique appearance, being broad and spade-like. In three of 18 *P. platyrhinos*, and in ten of 35 *P. cornutum* examined, the median process was absent. In the other

Table 4. Variation in the length of the interclavicle median process (in mm) among the species of *Phrynosoma*. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation).

Species	N	$\bar{X}$	S.E.	S.D.	Range
<i>P. asio</i>	6	2.45	—	—	1.78–3.04
<i>P. braconneri</i>	4	2.21	—	—	1.63–3.00
<i>P. cornutum</i>	35	0.76	0.18	1.04	0–4.75
<i>P. coronatum</i>	19	1.72	0.16	0.68	0.34–3.55
<i>P. ditmarsii</i>	3	1.30	—	—	1.11–1.57
<i>P. douglassii</i>	14	2.32	—	—	0.86–4.05
<i>P. mcallii</i>	4	1.50	—	—	1.06–1.96
<i>P. modestum</i>	1	1.20	—	—	—
<i>P. orbiculare</i>	6	2.64	—	—	0.80–4.84
<i>P. platyrhinos</i>	18	0.71	0.10	0.44	0–1.42
<i>P. solare</i>	13	2.40	—	—	1.03–3.99
<i>P. taurus</i>	2	1.30	—	—	1.28–1.31

sceloporine genera and the crotaphytines, the median process of the interclavicle is relatively long (Presch, 1969; Weiner and Smith, 1965).

CAUDAL VERTEBRAE. Unlike typical lizards, *Phrynosoma* are squat reptiles with relatively short tails. In some species of horned lizards, the reduction in tail length is extreme. I have counted the number of caudal vertebrae (character CAUD) in several species and compared my counts with those from Presch (1969:table 1). I have substituted my counts only in cases where the previous information is believed questionable, or where my data have changed the observed range of variation. In the data presented below, each species is followed by the sample size and range in number of caudal vertebrae in parentheses.

The tail is very short in two species, *Phrynosoma braconneri* (4, 10–11) and *P. taurus* (4, 9–12). The tail is considered short in *P. ditmarsii* (1, 14). The tail is of moderate length in the remaining species, with considerable overlap in the observed range of variation: *Phrynosoma asio* (3, 20–22); *P. cornutum* (25, 16–22); *P. coronatum* (9, 19–23); *P. douglassii* (40, 19–22); *P. mcallii* (9, 21–24); *P. modestum* (6, 16–20); *P. orbiculare* (5, 18–24); *P. platyrhinos* (22, 20–24); and *P. solare* (13, 19–20). On the basis of typical lacertilian tail-body proportions, a moderate tail length in *Phrynosoma* is the ancestral character state, and any reduction in the number of caudal vertebrae (<16) is considered a derived condition.

EXTERNAL MORPHOLOGY

EXTERNAL NARIS. The external naris is situated (character PNAR) on the line of the canthus rostralis in *Phrynosoma asio*, *P. ditmarsii*, *P. douglassii*, and *P. orbiculare*. The external naris lies above the canthus rostralis, i.e., both nares are situated well within the canthal lines and slightly closer to the orbits in *P. braconneri*, *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, *P. solare*, and *P. taurus*. The character is variable among the subspecies of *P. coronatum*.

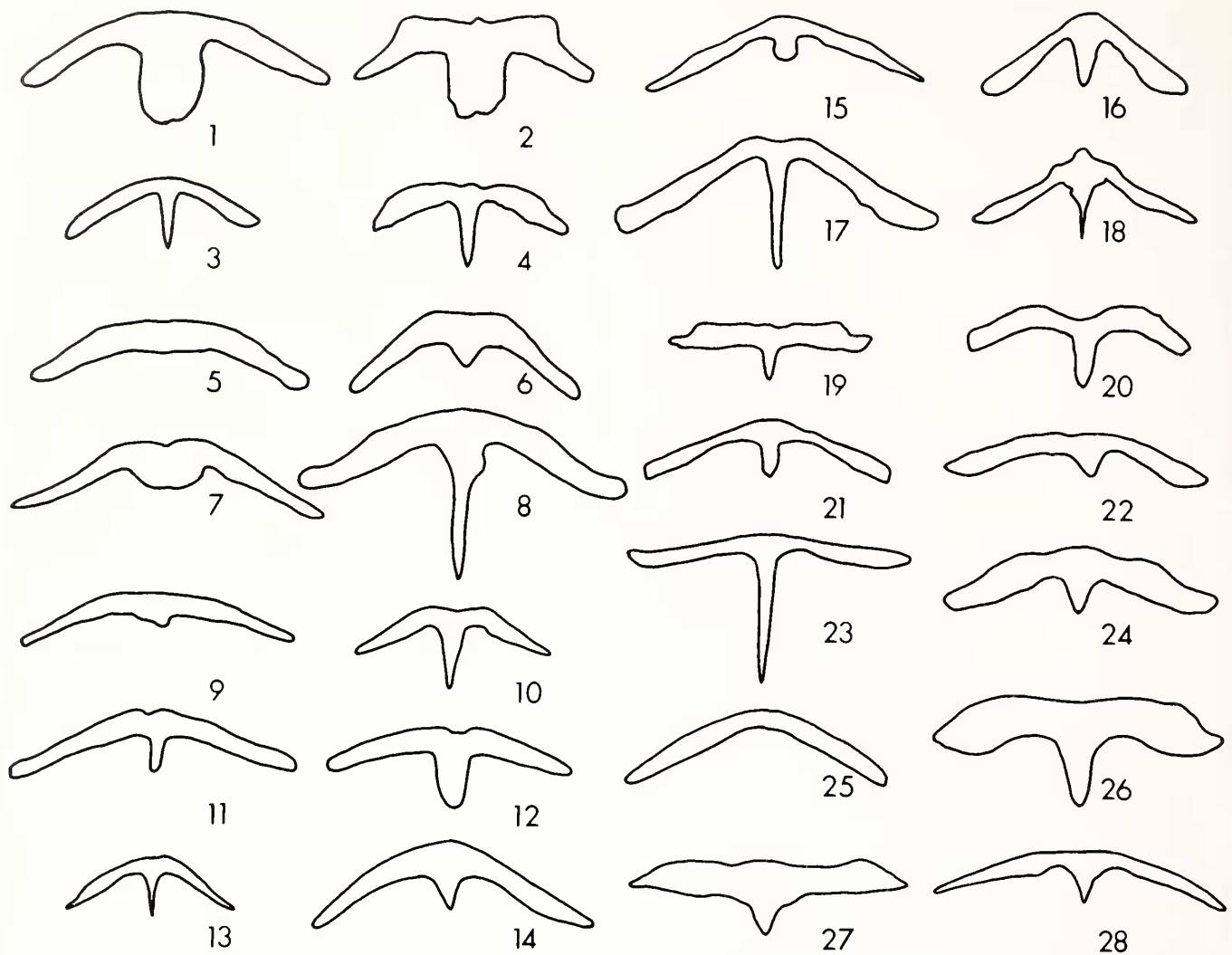


Figure 8. Variation in the length and shape of the medial process of the interclavicles of *Phrynosoma* species. The species are *P. asio* (1, AMNH 74839; 2, MVZ 13771), *P. braconnieri* (3, UTA 10281; 4, USNM 165694), *P. cornutum* (5, UMMZ 149115; 6, KU 20993; 7, AMNH 76188; 8, MVZ 78386), *P. coronatum* (9, MCZ 131759; 10, MVZ 137775; 11, LACM 127268; 12, MVZ 272), *P. ditmarsii* (13, TRV 2537; 14, UAZ 35511), *P. douglassii* (15, UMMZ 149120; 16, UMMZ 138825; 17, KU 13943; 18, UMMZ 149119), *P. mcallii* (19, MVZ 111509; 20, MCZ 44822), *P. modestum* (21, AMNH 74597), *P. orbiculare* (22, MCZ 11313; 23, RRM 2379), *P. platyrhinos* (24, MVZ 64187; 25, RRM 2323), *P. solare* (26, KU 13941; 27, AMNH 2579), and *P. taurus* (28, UTA 17129).

Schmidt (1922) noted that in *P. c. jamesi* and *nelsoni*, the naris lies just below the canthus rostralis, possibly due to enlargement of the narial aperture. However, Reeve (1952) described the naris as located above the canthal line in *P. c. schmidtii* (including *nelsoni*) and in *P. cerroense*, on the canthal line in *P. c. blainvillii*, *frontale*, and *jamesi*, and on or slightly above the line in *P. c. coronatum*. Cope (1900) stated that the nares lie on the canthal lines in *P. cerroense*. In the other sceloporine genera, the nares lie slightly within the canthi, but in the crotophytines they are located essentially on the canthi.

The external nares pierce the snout laterally, or with a slight dorsolateral angle, in *Phrynosoma asio*, *P. coronatum*, *P. douglassii*, and *P. orbiculare*. The nares show a pronounced

dorsolateral angle of entry in *P. ditmarsii*. The nares enter dorsally in *P. braconnieri*, *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, *P. solare*, and *P. taurus*. The external nares open more or less dorsolaterally in the other sceloporines, but laterally in the crotophytine genera.

In *Phrynosoma*, the location and angle of entry of the external nares are not totally independent characters. Nares located well within the canthal lines are dorsally pierced, whereas nares situated on the canthi, or nearly so, have almost lateral to distinctly dorsolateral entry. Also, location of the nares may be developmentally correlated with the spatial arrangement of the nasal, prefrontal, and maxillary elements. In *Phrynosoma* with nares situated on the canthi and somewhat distant from the orbits, the nasals and maxillae are in

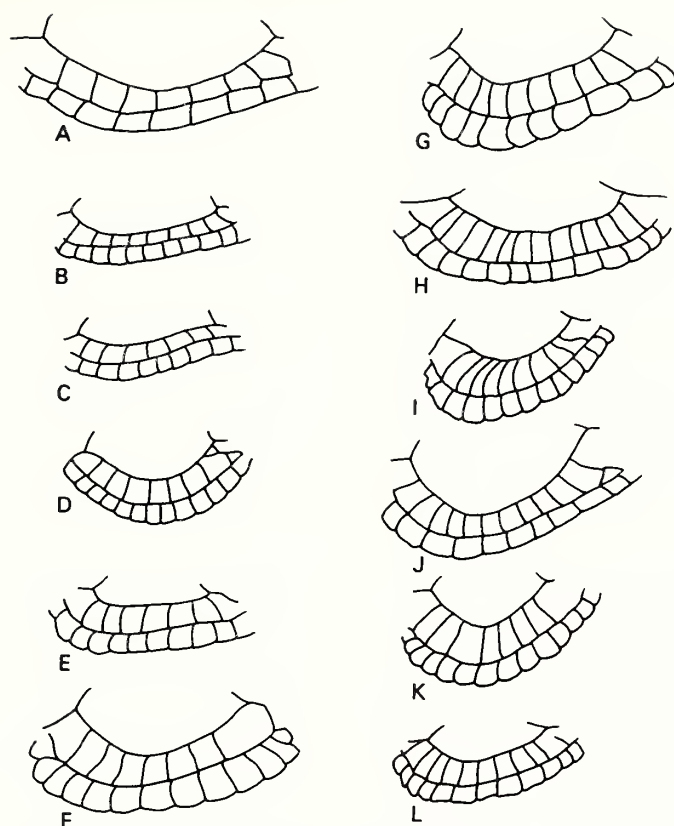


Figure 9. Variation in the width of the double row of ciliaries, from the left lower eyelid of *Phrynosoma* species. The species are A, *P. asio* (RRM 1756); B, *P. taurus* (UTA 11388); C, *P. braconnieri* (UTA 4222); D, *P. dimarsi* (RRM, no number); E, *P. orbiculare* (RRM 2377); F, *P. douglassii* (RRM 2306); G, *P. cornutum* (RRM 2094); H, *P. coronatum* (RRM 2331); I, *P. mcallii* (RRM 2239); J, *P. solare* (RRM 2376); K, *P. platyrhinos* (RRM 2129); L, *P. modestum* (RRM 2290).

contact. The posterior displacement (toward the orbits) of the nares within the canthi, however, has apparently excavated the nasal bones, resulting in the loss of contact between the nasals and maxillae (a derived character state; see discussion of polarity under Maxilla). In other sceloporines, including the sand lizards, the two elements maintain contact because the nares, although placed slightly within the canthi, are relatively distant from the orbits.

The out-group evidence would indicate that dorsolaterally pierced nares situated slightly within the canthi represents the ancestral morphology, but this combination of character states is not clearly seen in *Phrynosoma*. The morphology closest to it is nares pierced somewhat dorsolaterally and variably located on or near the canthi. On the basis of the developmental correlation between location of the nares and the positional relationship between the nasals and maxillae, the derived morphology is probably dorsally pierced nares located well within the canthi and somewhat posteriorly displaced.

CILIARIES. The ciliaries are small, rectangular scales which form a double row along the margin of the upper and lower eyelids. In *Phrynosoma*, there is variation in the width of the double rows, as well as in the configuration of the edge of the outer row. In the outer row, the slightly flattened scales

may produce a crenate, weakly crenate, or even edge. The even edge is more prevalent than the crenate border within each species of *Phrynosoma*. Also, the configuration of the edge may change from an even border centrally to weakly crenate near the corners of the eye where the upper and lower eyelids meet (Fig. 9, Table 5). *Phrynosoma mcallii* and *P. platyrhinos* have the widest ciliary scale rows, whereas *P. asio*, *P. braconnieri*, and *P. taurus* have the narrowest. Species of *Phrynosoma* inhabiting sandy environments tend to have wide or moderately wide ciliary scale rows. This also holds true for the sand-dwelling sceloporine genera *Callisaurus*, *Holbrookia*, *Uma*, and the agamid *Phrynocephalus*. The wide ciliary scales may offer protection for the eyes in such environments.

In *Crotaphytus* and *Gambelia*, the edge configuration of the upper row of ciliaries is flat or weakly denticulate; the lower eyelid has a denticulate border of cone-shaped scales which are slightly flattened in *Gambelia*. *Petrosaurus* has a similar morphology. In the sand lizards, e.g., *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*, the upper eyelid has a crenate to weakly denticulate edge; on the lower eyelid, the outer row of scales produce a denticulate border, and they are flattened rather than cone-shaped. In *Urosaurus*, a crenate border is seen, but the scales are bead-like rather than flat-

Table 5. Variation in the width of the ciliary scale rows from the lower eyelid of *Phrynosoma*. The ciliary row width is expressed as a percentage of the horizontal diameter of the eye opening. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation).

Species	N	$\bar{X}$	S.E.	S.D.	Range
<i>P. asio</i>	21	24.7	0.58	2.67	20.0–30.9
<i>P. braconneri</i>	12	25.9	—	—	23.5–30.0
<i>P. cornutum</i>	17	36.1	0.66	2.75	31.6–41.1
<i>P. coronatum</i>	17	40.2	0.75	3.13	35.3–45.0
<i>P. ditmarsii</i>	8	31.2	—	—	25.0–37.0
<i>P. douglassii</i>	17	43.7	0.71	2.94	41.7–50.0
<i>P. mcallii</i>	16	46.6	0.90	3.63	39.0–51.8
<i>P. modestum</i>	20	41.5	0.78	3.50	35.5–47.6
<i>P. orbiculare</i>	25	36.5	1.04	5.21	27.2–50.0
<i>P. platyrhinos</i>	14	46.2	—	—	40.9–50.9
<i>P. solare</i>	12	30.3	—	—	27.9–34.2
<i>P. taurus</i>	8	26.9	—	—	22.9–29.2

tened. Among the sceloporines, *Uta* has a ciliary scale morphology similar to that of *Phrynosoma*; the scales in the outer row are slightly flattened and form a weakly crenate to even edge.

Owing to the morphological diversity of the ciliaries in other sceloporine genera, out-group comparisons provide little useful information on the directionality of character states. However, the widened double row of scales with a denticulate border (produced by the outer row of flattened scales) appears to be an elaboration of the widened rows bearing a crenate border. In turn, the latter morphology seems to be derived from the narrow double scale row with an even edge. The narrow, even-edged row is a relatively simple morphology and may represent the ancestral condition in *Phrynosoma*.

SUPRALABIALS. There is interesting variation in shape and orientation of the supralabial scales. The infralabials are less differentiated and were not studied. In *Phrynosoma orbiculare*, the supralabials are more or less diagonally oriented, slightly flaring, and the scale row produces a scalloped buccal margin (character SLAB). The surface of each scale may be relatively smooth, or have one or two lengthwise keels which are weak and rounded. The supralabials are similar in *P. douglassii*, but the diagonal orientation may be weak or absent. The surface of the scales may be smooth, or have slight rugosities or weak keels. In juveniles of both species, the keels may be more distinct, and the buccal margin is more strongly scalloped.

In *Phrynosoma asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*, the supralabials have a slight diagonal orientation or none at all, and are not flared. The buccal margin of the scale row is weakly scalloped or flat in *P. asio*, but more or less scalloped in the other three species. The scale surface may have slight rugosities or weak, lengthwise, double keels. In juveniles of the four species, the keels are more distinct and the buccal margin more strongly scalloped than in adults (except juveniles of *P. asio* with weakly scalloped margins).

In *Phrynosoma cornutum*, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*, the supralabials have little or no diagonal orientation. The buccal margin of the scale row is scalloped anteriorly to dentate posteriorly, or dentate throughout (Fig. 10). The buccal margin is more extensively dentate in the southern races of *P. coronatum* (*coronatum* and *jamesi*) than in the northern *blainvillii* and *frontale* in which the dentate scales tend to be restricted posteriorly. The surface of the scales varies from smooth to slightly rugose; the rugosities tend to converge toward the apex of the dentate scales. Single or double lengthwise keels may be strong, weak, or absent on the supralabials of *P. coronatum*, however, the keels are acute and very distinct in juveniles. The apex of each dentate scale may bear a spine in juveniles of *P. mcallii*.

The ancestral condition is considered to be supralabials with a slight diagonal orientation and with a weakly scalloped to nearly flat buccal margin. This conclusion, however, is equivocal since only the sand lizards among the sceloporine out-groups have a similar morphology (Maddison et al., 1984). The slightly tilted supralabials of some *Phrynosoma* is reminiscent of the more highly specialized supralabial morphology characteristic of the sand lizard genera. No other sceloporines share this similarity. Thus, tilted supralabials may represent another synapomorphy between the two groups. In the sand lizards, the oblique supralabials are enlarged and apparently are an adaptation for efficient "shimmy-burial." In *Phrynosoma* this function appears, on the basis of behavioral observations, to have been taken over by the chin-shields.

POSTLABIALS. The postlabials (character PLAB) are enlarged scales which are continuous with the infralabials posteriorly. *Phrynosoma orbiculare* and *P. douglassii* have about three flattened, triangular postlabials which enlarge posteriorly in the series, and which project upward. In *P. coronatum*, there is a single very large, flattened, triangular postlabial (=subtrical) which is directed horizontally. In *P. ditmarsii* and *P. taurus*, the postlabials are slightly enlarged, convex, triangular scales, with the keeled edge of the row directed nearly horizontally. *Phrynosoma asio* has a similar morphology, but the scales are less enlarged, or subequal to the infralabials. In *P. braconneri*, the scales are larger than in *P. ditmarsii* and *P. taurus*, more flattened than convex, and less pointed. In *P. cornutum*, *P. modestum*, and *P. solare*, the postlabials are slightly enlarged, or subequal, compared with the infralabials, and are convex, triangular, usually projecting slightly upward. In *P. mcallii* and *P. platyrhinos*, the postlabials are not differentiated from the infralabials, or may be reduced in size.

In other sceloporines (except the sand lizards) and the crotaphytines, the postlabials are similar to the infralabials, or become reduced in size. In the sand lizard genera, the postlabials are more or less enlarged, but in shape are unlike the scales of *Phrynosoma*. Enlarged postlabials are probably plesiomorphic in *Phrynosoma*. This conclusion, however, is equivocal since only the sand lizards among the sceloporine out-groups have a similar postlabial morphology.

POSTRICTAL. The most posterior scale in the postlabial

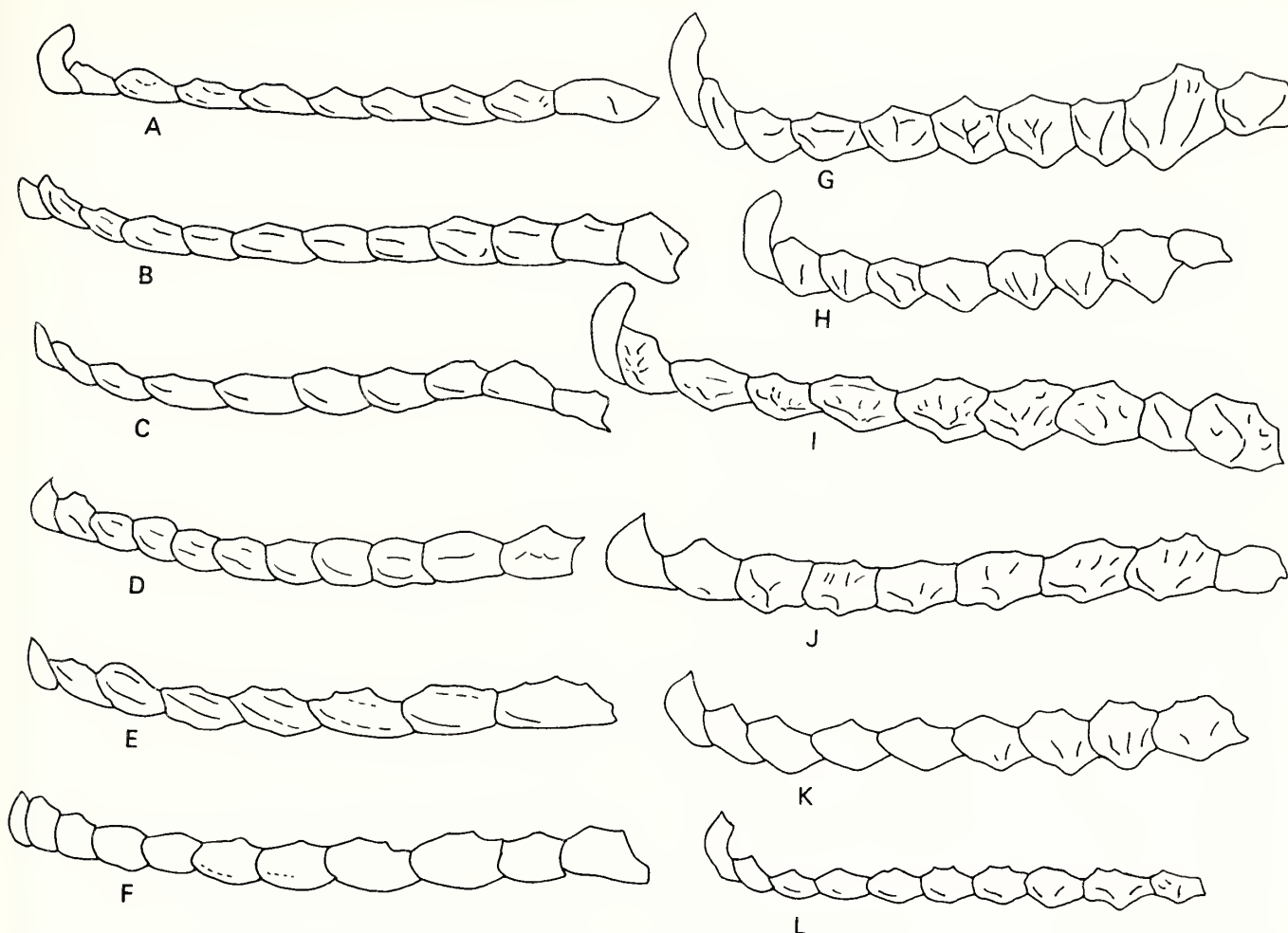


Figure 10. Variation among the species of *Phrynosoma* in the supralabial scale row morphology (left lateral aspect). The species are **A**, *P. asio* (RRM 1754); **B**, *P. taurus* (UTA 9092); **C**, *P. braconnieri* (UTA 4222); **D**, *P. ditmarsii* (RRM 2403); **E**, *P. orbiculare* (RRM 2377); **F**, *P. douglassii* (RRM 2310); **G**, *P. cornutum* (RRM 2094); **H**, *P. mcallii* (RRM 2239); **I**, *P. solare* (RRM 2406); **J**, *P. coronatum* (RRM 2331); **K**, *P. platyrhinos* (RRM 2407); **L**, *P. modestum* (RRM 2082).

series is morphologically distinguishable from the anterior scales in some species. This scale is called the postrictal, and its presence near the anteroventral border of the tympanum has been noted in several species, e.g., *P. coronatum*, *P. douglassii*, and *P. orbiculare* (Smith, 1946; Reeve, 1952). In these species, the postrictal may vary in size, but is usually large and cone-shaped. On the basis of location and shape, I have also identified a small postrictal in *P. solare*, *P. asio*, and *P. ditmarsii*. The scale is weakly keeled in *P. solare*, but in the latter two species, it has strong, multiple keels. The postrictal is apparently absent in the remaining species of *Phrynosoma*, as well as in the sceloporine out-groups.

CHINSHIELDS. In *Phrynosoma*, the chinshields (character CHIN) are enlarged, triangular scales extending posteriorly from the mental as a paired series (Fig. 11). In *P. cornutum*, *P. coronatum*, *P. mcallii*, and *P. solare* the chinshields are greatly enlarged, forming a strongly peaked or dentate series. In *P. modestum* and *P. platyrhinos*, the chin-

shields are somewhat shorter and blunter. In these six species, the scales tend to project laterally or slightly ventrolaterally. In *P. orbiculare* and *P. douglassii*, the scales are much smaller, slightly flattened, and produce a less strongly peaked edge. The chinshields tend to project laterally, or slightly upward. In *Phrynosoma asio*, *P. braconnieri*, and *P. taurus*, the chinshields are convex and scarcely project; instead, the keeled edge of the scale row produces a nearly even margin. In *P. ditmarsii*, the last two or three chinshields are peaked and project ventrally or nearly so. However, the morphology of the more anterior chinshields closely resembles that of *P. asio*, *P. braconnieri*, and *P. taurus*.

Other sceloporines have a short series of chinshields that are subquadrate or rounded, not triangular as in *Phrynosoma*, and which diminish in size posteriorly; in *Phrynosoma* they enlarge. I am not certain that the chinshields of *Phrynosoma* are homologous to those of other sceloporines. In horned lizards the chinshields are located along the margin of the

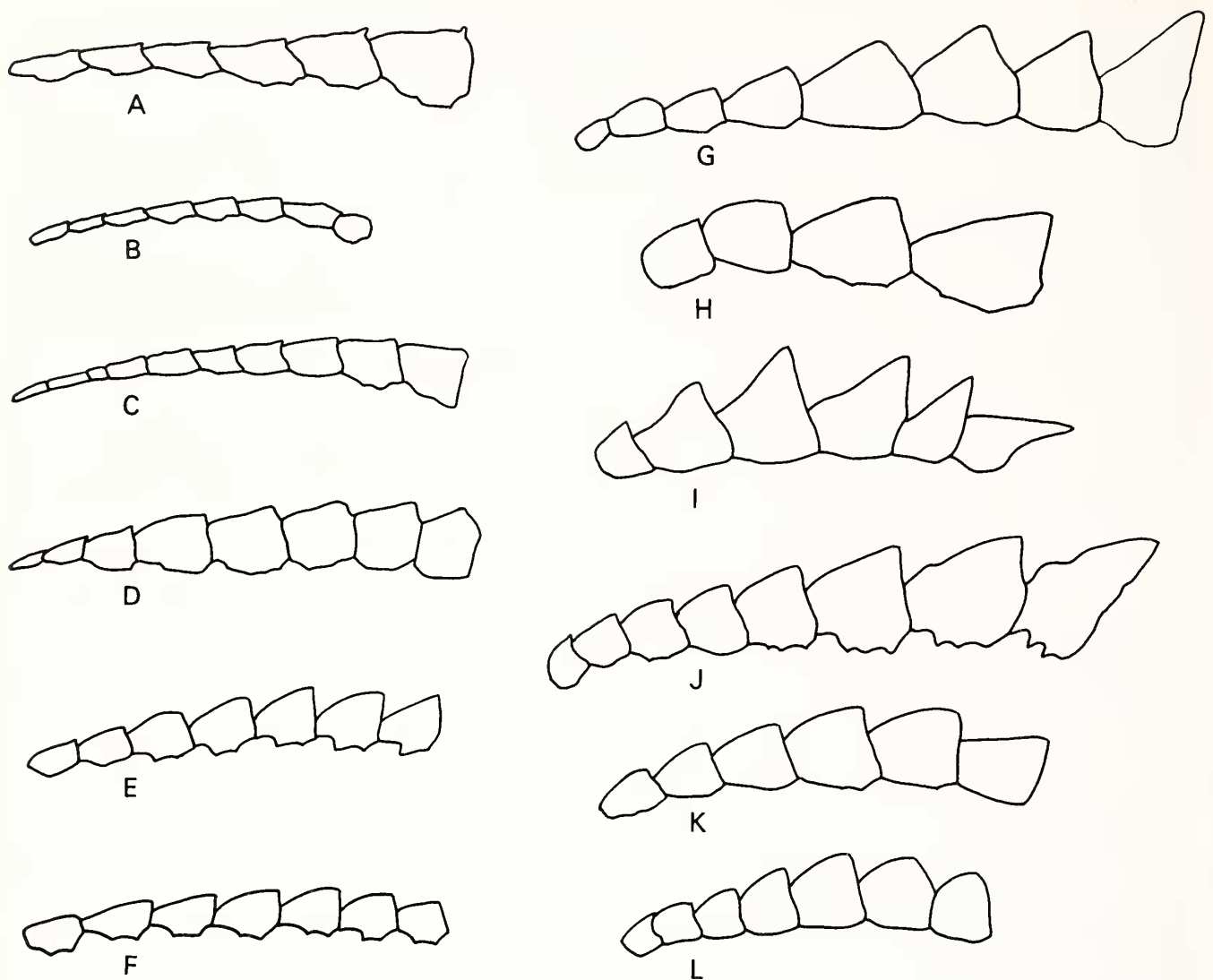


Figure 11. Ventral aspect of the left row of chinshields in *Phrynosoma*. The species are A, *P. asio* (RRM 1754); B, *P. braconnieri* (UTA 4222); C, *P. taurus* (UTA 9092); D, *P. ditmarsii* (RRM 2403); E, *P. orbiculare* (RRM 2377); F, *P. douglassii* (RRM 2265); G, *P. cornutum* (RRM 2094); H, *P. coronatum* (RRM 2178); I, *P. mcallii* (RRM 2236); J, *P. solare* (RRM 2336); K, *P. platyrhinos* (RRM 2039); L, *P. modestum* (RRM 2082).

lower jaws, but in other sceloporines they are more medially located. The chinshields of *Phrynosoma* may have been derived from a more lateral series of sublabials. In some *Phrynosoma* the chinshields contact the infralabials; the intervening sublabials have been eliminated. In the sand lizard group, there is a series of sublabials which tend to enlarge posteriorly, and which may correspond to the chinshields of *Phrynosoma*.

GULARS. In some species of *Phrynosoma*, one or more longitudinal series of enlarged gulars is present on either side of the throat. In *P. douglassii*, *P. modestum*, and *P. orbiculare*, the longitudinal rows of enlarged scales are absent, the gulars being equal or subequal in size. In *P. braconnieri*, *P. ditmarsii*, and *P. taurus* a single, short row of slightly enlarged gulars

is present on either side of the throat, but the enlarged scales are usually absent in *P. braconnieri*. A more extensive, single row of enlarged gulars is seen in *P. cornutum*, *P. mcallii*, *P. platyrhinos* (may be absent or present), and *P. solare*. In some *P. solare* there is a second, more medial longitudinal series of slightly enlarged scales. In *Phrynosoma asio* and *P. coronatum*, there are three to five longitudinal rows of enlarged gulars. The enlarged gulars project (character ENGPG) vertically, or nearly so, in *P. asio*, *P. braconnieri* (when present), *P. ditmarsii*, and *P. taurus*. In the remaining species with enlarged gulars, the scales lie flat against the throat. Other sceloporines and the crotophytines lack rows of enlarged gulars, except those differentiated as sublabials, postmentals, and chinshields.

The gular scales are keeled (character KEGU) in *Phrynosoma asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*. The gular scales are not keeled in the remaining species. Cope (1900) and Reeve (1952) described the gulars in *P. boucardii* (= *P. orbiculare boucardii*) as being feebly keeled. The scales have a slight convex surface, but in my opinion, they are not keeled. The ancestral character state is judged to be smooth gulars on the basis of comparisons with the other sceloporines and the crotophytines.

VENTRALS. The ventral scales are smooth (character VENS) in *Phrynosoma coronatum*, *P. douglassii*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, and *P. solare*. The ventrals are weakly keeled in *P. cornutum*, the keels being broad and obtuse. In *Phrynosoma asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*, the ventrals are sharply carinate. Several authors (Gentry, 1885; Smith, 1946; Reeve, 1952) erroneously described the ventrals of *P. solare* as being keeled. Cope (1900) and Van Denburgh (1922) noted correctly that the abdominal scales are smooth, with keeled scales being restricted to the extreme anterior chest area. Smith (1946) also stated that the ventrals are feebly keeled in *P. mcallii*, but other authors have correctly noted that the ventrals are smooth. The ancestral character state is smooth ventrals on the basis of out-group comparisons.

In *Phrynosoma asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*, the ventral scales are mucronate (character MVEN). The mucrone is small, originating at the end of the keel, and projecting posteriorly and slightly upward. The ventrals are non-mucronate in the remaining species, including *P. cornutum* which has feebly keeled ventrals. Non-mucronate ventrals are considered to be the ancestral condition based on comparisons with the out-groups.

LATERAL ABDOMINAL FRINGE ROWS. The presence of abdominal fringe scales is unique to *Phrynosoma*. An upper row of fringe scales (character UFRO) is present in all species of *Phrynosoma*, except *P. modestum*. A complete lower row of abdominal fringe scales (character LFRO) is present in *P. asio*, *P. cornutum*, and *P. coronatum*. A less extensive lower row of slightly enlarged fringe scales is present in *P. mcallii*. The remaining species lack a lower row of fringe scales. Gentry (1885) incorrectly described *P. mcallii* as altogether lacking abdominal fringe scales, and *P. solare* as having two rows. Cope (1900), Van Denburgh (1922), and Reeve (1952) also described *P. solare* as having two rows, but Smith (1946) stated that it had one. I have noted that in some specimens, some of the extreme lateral belly scales are enlarged, but these do not form a regular series. I conclude that *P. solare* lacks a second, lower row of fringe scales.

The single lateral fringe row which some horned lizard species have is clearly identified as the upper row because it is bordered by dorsals above and lateral granular scales below, and it is positioned along the distal ends of the abdominal ribs. The lower row is situated below the rib line and is bordered superiorly by granular scales and inferiorly by imbricate ventrals.

The absence of the upper fringe row would have to be judged the ancestral character state based on out-group comparisons. However, the cladistic results suggest that its ab-

sence in *P. modestum* is an autapomorphic loss (see Evolutionary Patterns of Characters). Absence of the lower fringe row is judged plesiomorphic by the out-group rule.

TYMPANUM. The tympanum (character TYMP) is exposed in all species of *Phrynosoma* except *P. mcallii* in which it is concealed by a scaly integument, and in *P. modestum* and *P. platyrhinos* in which it may be completely hidden, partly exposed, or completely exposed. Smith (1946) did not note the variation of this character in *P. modestum*. The exposed tympanum is the ancestral character state on the basis of out-group comparisons.

DORSALS. The dorsal scales of *Phrynosoma* are heterogeneous, being composed of enlarged, carinate, spinose scales, interspersed among smaller scales that do not form regular transverse rows. The smaller scales may be smooth or carinate, rounded or irregular in shape, with some variation in size on any individual horned lizard. The smaller dorsals are of little systematic importance, at least at the gross morphological level.

The enlarged dorsals (character DORS), however, are variously modified among the species of *Phrynosoma*. In *P. cornutum*, *P. coronatum*, *P. douglassii*, and *P. orbiculare*, the largest dorsals are slightly flattened, conical scales which taper to a spine. There are three keels, a prominent median dorsal (anterior) keel, and two lateral ones, except in *P. cornutum*, which has a fourth keel on the posterior surface of the base of the scale. The spinose scales are slightly smaller in *P. orbiculare* and *P. douglassii* than in the other two species. These four species have slightly smaller, conical spines located dorsolaterally. In *Phrynosoma solare*, the largest scales in the middorsal area are somewhat depressed and rounded, with two short lateral keels that meet the median keel at nearly right angles near the posterior margin; a spine arises more or less abruptly from the median keel. There is little or no free edge to the scales. Dorsolaterally, the enlarged scales become more conical and tapering, as in the preceding species. In *P. modestum* and *P. platyrhinos*, the enlarged dorsals are rounded to slightly widened, flat, with a free posterior edge and median keel (the keel is absent in some *P. platyrhinos*). The scales are mucronate in *P. platyrhinos*, but in *P. modestum*, they taper without a distinct spine. In *P. mcallii*, dorsals of large and intermediate size are distinctly widened with two lateral keels and with or without a median keel. A free posterior edge is more or less developed by the lateral keels in the largest scales. The scales may or may not terminate abruptly in a spine. In *Phrynosoma asio*, the largest scales in the middorsal region are rounded, strongly depressed, with a median keel and two short lateral keels near the posterior margin. There is no free edge, and the scales may or may not be mucronate. The enlarged scales form a paravertebral series, becoming more elevated and conical near the rump and on the tail. In some specimens of *P. asio*, moderately elevated scales are found middorsally on the body as well. In the dorsolateral areas, there are enlarged, conical scales which taper to a spine; the scales are strongly erect and bear multiple keels. In *P. braconneri*, *P. ditmarsii*, and *P. taurus*, the largest scales in the middorsal region are rounded, with a straight or slightly rounded posterior margin. There

is a median keel and two short lateral keels which produce little or no free edge. The scales are depressed and terminate more or less abruptly in a spine, though slightly more tapering in *P. ditmarsii* and some samples of *P. braconneri*. In all three species, the rump and dorsolateral areas have similar, but somewhat more conical scales.

In *Phrynosoma braconneri* and *P. taurus*, the dorsal area of the neck has two paravertebral rows of enlarged, keeled, juxtaposed scales (character NUCH). In each row there are three to four, seldom two or five, scales. *Phrynosoma douglassii* and *P. orbiculare* also have a paravertebral series of enlarged scales, but the scales are separated from each other and differ in shape, being more spinose.

The enlarged, depressed, carinate dorsals (in the middorsal area) of *Phrynosoma asio* may represent the ancestral condition in *Phrynosoma*, and subsequent adaptive modification for a defensive function would logically have involved progressive stages of elevation and elongation into tapered, spinose scales.

PHYLOGENETIC ANALYSIS

The monophyly of *Phrynosoma* is supported by the following diagnostic characteristics: 1) horns on the parietal, squamosal, and other cranial elements (reduced in some species); 2) posteriorly directed prefrontal process present; 3) anteriorly directed frontal process present; 4) temporal process of the jugal is expanded; 5) the retroarticular process is more or less vertically flattened (nearly absent in some species); 6) caudal vertebrae lack autotomic septa; 7) phalangeal formula for digits 4 and 5 of manus is 2:3:4:4:2, and for digit 5 of pes is 2:3:4:5:3; 8) head scales generally small, not differentiated into enlarged series; 9) several subocular scales, small and subequal in size; 10) length and overlap of superciliary scales reduced; 11) one or two rows of enlarged, lateral abdominal fringe scales (absent in one species); 12) dorsal scales on body and tail not arranged as distinct, transverse rows; and 13) dorsal scales heterogeneous, with enlarged, spinose scales interspersed with smaller scales (Etheridge and de Queiroz, in press; Etheridge, 1964; Presch, 1969). All of these characteristics are believed to be autapomorphies for the genus *Phrynosoma*.

CHARACTERS

A total of 36 characters was used in the phylogenetic analysis. The discrimination between derived and ancestral character states was accomplished primarily by the "out-group" method (Watrous and Wheeler, 1981; Maddison et al., 1984). *Phrynosoma* is a member of the sceloporines and is the sister group of the sand lizard assemblage (Presch, 1969; Arnold, 1984). The first out-group is therefore comprised of the sand lizards (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*). The remaining genera of sceloporines represent two informal groups, the *Uta-Urosaurus-Sator-Sceloporus* line, and *Petrosaurus*. A fourth out-group consists of the crotaphytines (*Crotaphytus* and *Gambelia*) which was chosen because of their apparent relationship with the sceloporines by way of *Petrosaurus*. The crotaphytines and *Petrosaurus* are similar

in ciliary scale morphology (see External Morphology). Etheridge (1964) noted that the morphology of the interclavicle and sternal fontanelle of *Petrosaurus* is reminiscent of that seen in *Crotaphytus*. Etheridge also noted that *Crotaphytus* is similar to all sceloporines in having an unfused Meckel's groove and caudal vertebrae with a single transverse process anterior to the fracture plane. However, these similarities noted by Etheridge may be symplesiomorphies, or of questionable validity. Etheridge and de Queiroz (in press) consider the absence of an enlarged, middorsal scale row to be one derived character state shared by the crotaphytines and sceloporines. See Materials and Methods section for the list of out-group taxa. Character states observed to be prevalent in the external taxa were considered plesiomorphous. Characters unique to *Phrynosoma* posed some difficulty. Estabrook (1977) argued that a character state widely distributed within a taxon is probably primitive. Thus a character state widespread within *Phrynosoma* was probably present in the common ancestor of the group prior to its radiation. Wiley (1981), however, argued that in cases where the apomorphic state arises early in the evolution of a group, it will be observed in the majority of the taxa comprising the group. Application of the criterion would then lead to erroneous conclusions regarding character evolution. In cases for which the out-group evidence was absent or ambiguous, I avoided polarity assignments and the characters were entered "unordered" into the analysis (see below). Other criteria, however, such as fossil evidence could not be used due to the paucity of information.

Characters were selected on the basis of their information content for phylogenetic study. Conservative characters with differences among the species were chosen over those with high variability within species. Some variable characters were used wherein discontinuities in the variation across taxa permitted non-arbitrary delimitation of character states. Some of the characters used are multistate, with discrete values assigned. Ancestral character states were encoded as 0, while derived character states were assigned a value of 1 or greater. For qualitative multistate characters, it was unnecessary to determine the transformation sequence in all cases since the computer program used in this analysis (see Data Set Analysis) has the ability to treat unordered as well as ordered characters. Unordered characters were encoded as described above. Autapomorphic characters, though tabulated, were not used in the cladistic analysis, but were employed in the computation of patristic distances. The 36 characters with their defined states and numerical equivalents (in parentheses) are listed alphabetically below.

1. ANGU The angular bone is present (0), variably present or absent (1), or completely absent (2).
2. CAUD The number of caudal vertebrae is 16 to 24 (0), about 14 (1), or from 9 to 12 (2).
3. CHIN Chinshields are not peaked, row margin even or nearly so (0), row margin even, but peaked posteriorly (1), row margin weakly peaked (2), chinshields obtuse, with moderately peaked margin (3), or row margin strongly peaked (4).

4. DENS The dentary surface is smooth and rounded (0), or angular with protuberances or horns (1).
5. DORS Enlarged dorsals (in median area) are depressed, carinate, without a free posterior edge (0), flat, more or less carinate, with a free edge (1), or tapered, spinose scales (2).
6. ECTO The ectopterygoid is not expanded (0), or more or less expanded (1).
7. ENAR The external naris enters nearly laterally or somewhat dorsolaterally (0), strongly dorsolaterally (1), or dorsally (2). Entered as an unordered character in the cladistic analysis.
8. ENGP Enlarged gular scales are absent (0), or present and project horizontally (1), or vertically (2).
9. ICMP The interclavicle median process, when present, is more or less slender (0), or wide and spade-like (1). An autapomorphic character, used only in the computation of the distance tree.
10. JUSA The posterior border of the jugal has no discernible orientation (0), or the border slopes posteriorly (1), slopes anteriorly (2), or the posterior border is flat (3). Entered as an unordered character in the cladistic analysis.
11. JUSH The jugal is not expanded posteriorly (0), or it is expanded (1).
12. JUSU The jugal surface is smooth (0), rugose (1), with tuberosities (2), or with processes (3).
13. KEGU Gular scales are smooth (0), or keeled (1).
14. LFRO The lower row of abdominal fringe scales is absent (0), short (1), or extensive (2).
15. MAND The mandible is not expanded vertically (0), or is greatly expanded (1). An autapomorphic character, used only in the computation of the distance tree.
16. MVEN Ventral scales are non-mucronate (0), or mucronate (1).
17. NAMX The nasal process of the maxilla reaches the nasal bone (0), or the two elements are separated by the prefrontal (1).
18. NUCH Paravertebral rows of enlarged, juxtaposed nuchal scales are absent (0), or present (1).
19. PANO A deep notch at the posterior margin of the parietal is absent (0), or present (1). An autapomorphic character, used only in the computation of the distance tree.
20. PARS An enlarged, projecting scale at the base of the parietal horn is absent (0), present (1), or second parietal horn is present (2).
21. PLAB The postlabials are slightly enlarged, convex, more or less peaked (0), not enlarged, subequal to or smaller than infralabials (1), triangular scales enlarging posteriorly (2), or one greatly enlarged, triangular scale (3). Entered as an unordered character in the cladistic analysis.
22. PMAX The angle of ascent of the premaxilla from its base to the point of suture with the nasals is gradual (54.5–65.6°) (0), or steep (70.6–73.7°) (1).
23. PNAR The external naris is situated on the canthal line (0), variable in relation to the canthal line (1), or well above the canthal line (2). Entered as an unordered character in the cladistic analysis.
24. POST The postorbital is nearly vertical, with slight outward curvature (0), or slanted, with strong outward curvature (1).
25. RLIP A rostral lip is absent (0), or present (1).
26. RSFA The rostrifrontal angle is obtuse, with a gradual slope (0), or more or less acute, with an abrupt slope (1).
27. SBAR The supraorbital bar is incomplete (0), nearly complete (1), or complete (2).
28. SLAB The supralabial margin is more or less scalloped (0), or partly or entirely dentate (1).
29. SPLN The splenial bone is present (0), or absent (1). An autapomorphic character, used only in the computation of the distance tree.
30. SPOP Contact between the supraoccipital and the parietal is tripartite (0), or complete (1). An autapomorphic character, used only in the computation of the distance tree.
31. SQSH The squamosal forms a more or less rounded arch (0), or is elongate (1). An autapomorphic character, used only in the computation of the distance tree.
32. SUFO The supratemporal fossa is present throughout ontogeny (0), or becomes occluded late in post-embryonic ontogeny (1). An autapomorphic character, used only in the computation of the distance tree.
33. SURA The surangular surface is smooth and convexly rounded (0), has laterally directed horns (1), is expanded with an angular edge (2), or has ventrally directed horns (3).
34. TYMP Tympanum is exposed (0), variably exposed or concealed (1), or completely concealed (2).
35. UFRO The upper row of abdominal fringe scales is absent (0), or present (1). An autapomorphic character, used only in the computation of the distance tree.
36. VENS Ventral scales are smooth (0), weakly keeled (1), or strongly keeled (2).

The distribution of character states among the species of *Phrynosoma* is presented in Table 6. The table contains the original data set before recoding was performed (see below) to eliminate homoplasy in some characters.

DATA SET ANALYSIS

The computer program used to analyze the *Phrynosoma* data set is Phylogenetic Analysis Using Parsimony (PAUP, Version 2.4) written by Swofford (1985). Information concerning the algorithms used in PAUP, including search strategies and character-state optimization methods may be obtained directly from Swofford and from the user's manual written by him. A brief and cursory explanation of some of PAUP's features follows.

Table 6. Distribution of character states for 36 characters among the 12 species of *Phrynosoma* and one hypothetical ancestor.

	ANGU	CAUD	CHIN	DENS	DORS	ECTO	ENAR	ENG	ICMP	JUSA	JUSH	JUSU	KEGU	LFRO	MAND	MVEN	NAMX	NUCH	PANO	PARS	PLAB	PMAX	PNAR	POST	RLIP	RSFA	SBAR	SLAB	SPLN	SPOP	SQSH	SUFO	SURA	TYMP	UFRO	VEVS	
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>P. asio</i>	0	0	0	0	0	1	0	2	1	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	2	
<i>P. braconieri</i>	0	2	0	0	0	1	2	2	0	1	1	1	1	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	1	2	
<i>P. cornutum</i>	0	0	4	1	2	1	2	1	0	3	1	3	0	2	0	0	1	0	0	0	0	1	2	0	0	0	1	2	1	0	0	0	1	0	1	1	
<i>P. coronatum</i>	0	0	4	0	2	1	0	1	0	3	1	3	0	2	0	0	0	0	0	0	3	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0
<i>P. ditmarsii</i>	0	1	1	0	0	1	1	2	0	0	0	2	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>P. douglassii</i>	0	0	2	0	2	1	0	0	0	2	1	2	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>P. mcallii</i>	2	0	4	1	1	1	2	1	0	3	1	3	0	1	0	0	1	0	0	1	1	1	2	1	1	1	2	1	1	0	0	1	1	2	1	0	
<i>P. modestum</i>	1	0	3	1	1	1	2	0	0	3	1	3	0	0	0	0	1	0	0	1	0	1	2	1	1	1	0	1	0	0	0	0	1	1	0	0	
<i>P. orbiculare</i>	0	0	2	0	2	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>P. platyrhinos</i>	0	0	3	1	1	1	2	1	0	3	1	3	0	0	0	0	1	0	0	1	1	1	2	1	1	1	0	1	0	0	0	0	1	1	1	0	
<i>P. solare</i>	0	0	4	1	0	1	2	1	0	3	1	3	0	0	0	0	1	0	0	2	0	0	2	1	1	1	1	2	1	0	0	0	1	0	1	0	
<i>P. taurus</i>	0	2	0	0	0	1	2	2	0	1	1	1	1	0	0	1	1	1	0	0	0	0	2	0	0	0	2	0	0	0	1	0	2	0	1	2	

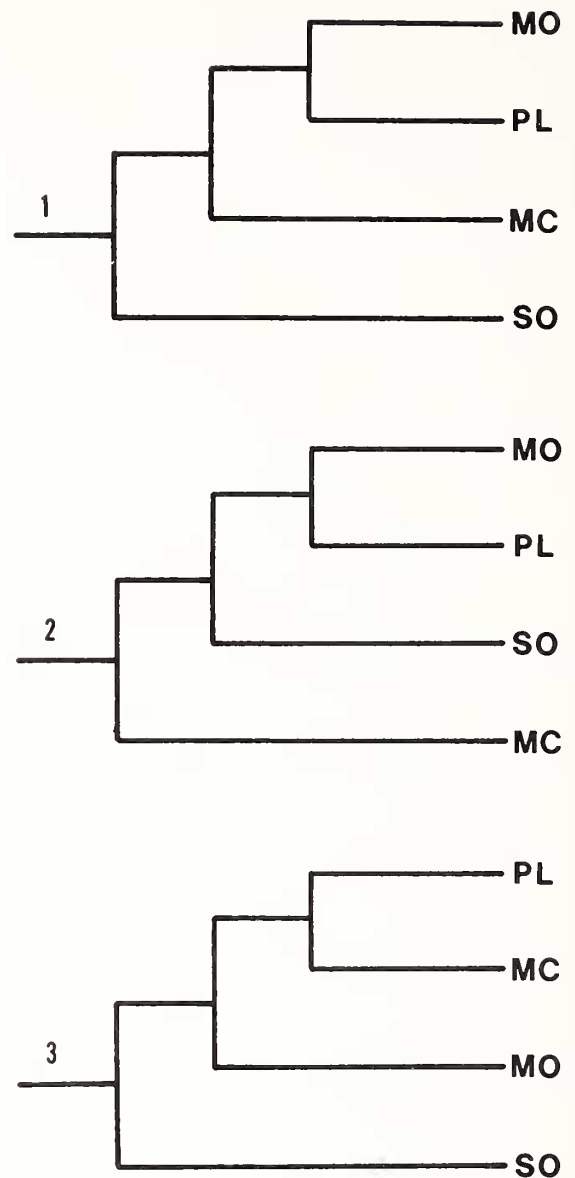


Figure 12. Three alternative branching arrangements for the possible relationships among *Phrynosoma mcallii* (MC), *P. modestum* (MO), *P. platyrhinos* (PL), and *P. solare* (SO). Branching arrangement number 1 is considered the most probable. See text for further discussion.

Computer programs using parsimony as an optimality criterion must seek a compromise between efficiency (speed and use of computer resources) and effectiveness (ability to optimize parsimony). Graham and Foulds (1982) argue that an efficient, exact solution is very unlikely and that a more promising approach is to develop heuristic techniques (those which do not guarantee parsimony but which are reasonably efficient). Nonetheless, PAUP includes two exact algorithms: an exhaustive search for all possible trees, and an improved branch-and-bound procedure (Hendy and Penny, 1982). These exact algorithms are applicable to relatively small data

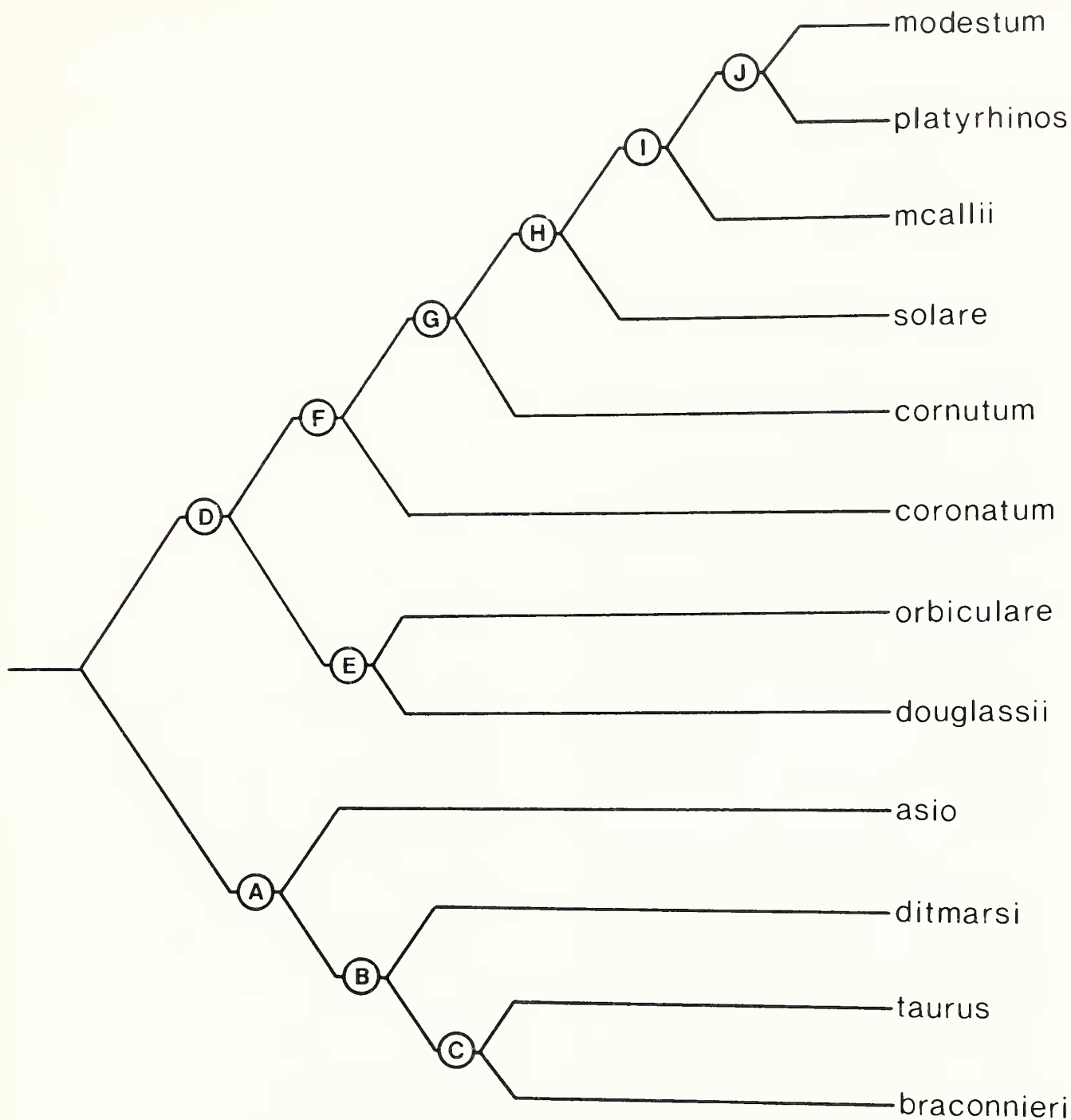


Figure 13. A computer-generated cladogram depicting the relationships of 12 species of *Phrynosoma*. See Tables 6, 7, and text for list of characters and further discussion.

sets, usually 12 or fewer taxa. For larger data sets, PAUP offers a wide array of options for obtaining a heuristic solution. Some parsimony methods impose restrictions on how character state changes may occur, such as a single origination of a character state, or prohibiting reversals. PAUP employs an unrestricted, maximum parsimony procedure. Further-

more, the program has the ability to treat unordered as well as ordered characters, but with the limitation that character states are assigned discrete values. Unordered multistate characters are those for which the transformation sequence or relationships of the states are unknown prior to analysis. Finally, PAUP has the ability to handle missing data, and

Table 7. List of synapomorphies for the cladogram of *Phrynosoma* (Fig. 13).

Node A	
ENGP:	Enlarged gulars project vertically.
KEGU:	Gulars acutely keeled.
MVEN:	Ventrals mucronate.
SURA:	Surangular expanded with an angular edge (except in <i>P. ditmarsii</i>).
VENS:	Ventrals acutely keeled.
Node B	
CAUD:	Caudal vertebrae reduced in number (about 14).
ENAR:	External nares enter strongly dorsolaterally.
Node C	
CAUD:	Caudal vertebrae further reduced (about 9–12).
CODS:	Coronoid overlaps dentary and surangular slightly (also at Node H).
ENAR:	External nares enter dorsally (also at Node G).
JUSA:	Jugal with flat, vertical posterior border.
JUSH:	Jugal expanded posteriorly (also at Node D).
JUSU:	Jugal surface rugose.
NAMX:	Nasals and maxillae not in contact (also at Node G).
NUCH:	Paravertebral rows of enlarged, juxtaposed nuchal scales.
PNAR:	External nares situated well above canthal lines (also at Node G).
Node D	
CHIN:	Chinshields small, produce weakly dentate margin.
DORS:	Enlarged dorsals tapered.
ENGP:	Enlarged gulars project horizontally.
JUSH:	Jugal is expanded posteriorly (also at Node C).
JUSU:	Jugal surface with tuberosities (also in <i>P. ditmarsii</i>).
POST:	Postorbital curves outward, skull flaring (except <i>P. cornutum</i>).
Node E	
ENGP:	Enlarged gulars secondarily lost (also in <i>P. modestum</i>).
JUSA:	Jugal with posterior border sloping posteriorly.
PLAB:	Postlabials flat, triangular, enlarged posteriorly, and directed upward.
Node F	
CHIN:	Chinshields enlarged, produce strongly peaked row margin.
JUSA:	Jugal with posterior border sloping anteriorly.
JUSU:	Jugal surface with processes.
LFRO:	Lower row of abdominal fringe scales extensive.
SLAB:	Supralabial margin partly or entirely dentate.
Node G	
DENS & SURA:	Dentary and surangular have laterally directed horns; i.e., chinshields acquire bony supports.
ENAR:	External nares enter dorsally (also at Node C).

Table 7. Continued.

NAMX:	Nasals and maxillae not in contact (also at Node C).
PMAX:	Spine of premaxilla ascends steeply from its base.
PNAR:	External nares situated well above canthal lines (also at Node C).
RSFA:	Rostrofrontal angle more or less acute.
SBAR:	Supraorbital bar is complete (also in <i>P. taurus</i>).
Node H	
CODS:	Coronoid overlaps dentary and surangular slightly (also at Node C).
DORS:	Dorsals flat, carinate, with free edge.
LFRO:	Lower abdominal fringe row secondarily lost.
PARS:	Enlarged, projecting scale at base of parietal horn.
RLIP:	Rostral lip present.
Node I	
ANGU:	Angular bone variably present or absent.
PLAB:	Postlabials subequal to or smaller than infralabials.
TYMP:	Tympanum partly concealed.
Node J	
CHIN:	Chinshields somewhat reduced, obtuse, less projecting.
SBAR:	Supraorbital bar secondarily incomplete.

can detect the existence of multiple equally parsimonious character-state reconstructions for the same tree.

Analysis of the *Phrynosoma* data set was performed with the following option settings: 1) no weights applied to the characters; 2) rooting with a designated hypothetical ancestor; 3) Simple Addition sequence, one of several options for determining the order in which operational taxonomic units (OTUs) will be added to the tree; 4) Farris optimization of character states assigned to hypothetical taxonomic units (HTUs); and 5) Global branch-swapping, an algorithm for rearranging tree topologies in search of shorter trees.

Analysis of the original data set yielded two most parsimonious trees, having nearly identical topologies. Both trees depict two groups of species within *Phrynosoma*, but differ in the arrangement of four species, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*. In a subsequent analysis, the characters NAMX, SBAR, PNAR, and ENAR were recoded to eliminate homoplasy. The characters were recoded by subdividing them into two different character sets (with alternative states) based on the primary dichotomy of the cladogram. The four homoplastic characters, as well as others, were retained because they helped to resolve relationships among some species. The analysis produced the two previously obtained trees, as well as a third, which differed, again, only in the arrangement of the aforementioned species (Fig. 12).

In an attempt to resolve the relationships of the four *Phrynosoma* species, computer analysis was performed on a subset of the original data matrix including the characters SBAR, PARS, CHIN, ENGP, TYMP, SUFO, ANGU, SPLN, UFRO,

Table 8. List of character consistencies for the characters (exclusive of autapomorphies) used in the cladistic analysis. A value of 1.0 indicates no homoplasy.

Character	Consistency	Character	Consistency
ANGU	0.667	NAMX	0.500
CAUD	1.000	NUCH	1.000
CHIN	0.667	PARS	1.000
DENS	1.000	PLAB	0.750
DORS	0.500	PMAX	0.500
ECTO	0.500	PNAR	0.500
ENAR	0.500	POST	0.500
ENGP	0.500	RLIP	1.000
JUSA	1.000	RSFA	1.000
JUSH	0.500	SBAR	0.286
JUSU	0.600	SLAB	1.000
KEGU	1.000	SURA	0.750
LFRO	0.286	TYMP	1.000
MVEN	1.000	VENS	0.667

LFRO, PMAX, DORS, and six additional, potentially useful characters. The six characters were deemed informative for the group of four taxa, but were excluded from the larger analysis because of homoplasy or high variability among the other species of *Phrynosoma*. The additional characters are: 1) CODS, the coronoid overlaps the dentary and surangular slightly (0), or none at all (1); 2) RICT, a small postriotal is present (0), or absent (1); 3) NSQH, two to three squamosal horns (0), or four horns (1); 4) CORA, supracoracoid foramen present (0), or absent (1); 5) MXOB, maxilla contacts orbital margin to a small (0), moderate (1), or large (2) extent; and 6) CILW, ciliary row width is moderately narrow (0), or wide (1). The character states for the six characters (in the order presented above) are: *P. mcallii* (110001); *P. modestum* (010121); *P. platyrhinos* (010011); and *P. solare* (101010). The ancestral states for these characters were determined using the remaining *Phrynosoma* species and the other sceloporines as out-groups. For further information on these characters, see the previous morphological descriptions.

Computer analysis of the data produced a single branching arrangement with a topology identical to the first arrangement in Figure 12. The first branching diagram is therefore accepted as the most probable. The entire phylogenetic reconstruction is presented as a cladogram (Fig. 13), which has a total length of 75.0 and a consistency index of 0.707. The synapomorphies supporting the cladogram are summarized in Table 7. One character listed in Table 7 (CODS) was used only for the analysis of the data subset to resolve the branching options (Fig. 12), but subsequently was mapped on the cladogram (Fig. 13). The character consistencies from the original data matrix are listed in Table 8.

The cladogram depicts two groups diverging from a common ancestor. One group, the “southern radiation” species, consists of *P. asio*, *P. braconneri*, *P. ditmarsii*, and *P. taurus*; the “northern radiation” group includes *P. douglassii*, *P.*

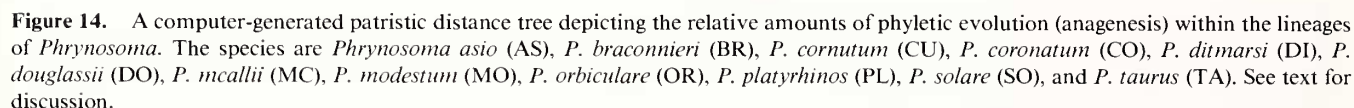
Table 9. Comparison of forelimb and hind limb length among selected species of *Phrynosoma*. Limb length is expressed as a percentage of snout–vent length. Abbreviations are N (sample size), $\bar{X}$ (mean), S.E. (standard error), and S.D. (standard deviation).

Species	N	$\bar{X}$	S.E.	S.D.	Range
Forelimb					
<i>P. douglassii</i>	14	32.60	0.387	1.45	29.87–35.00
<i>P. ditmarsii</i>	9	40.03	0.593	1.78	37.88–42.86
<i>P. braconneri</i>	36	39.41	0.438	2.62	34.69–45.95
<i>P. taurus</i>	19	39.67	0.514	2.24	33.72–43.33
Hind limb					
<i>P. douglassii</i>	14	44.11	0.722	2.69	39.51–48.68
<i>P. ditmarsii</i>	9	53.38	1.116	3.34	48.00–57.69
<i>P. braconneri</i>	34	53.27	0.533	3.11	48.98–60.42
<i>P. taurus</i>	19	53.89	1.155	5.02	46.51–69.70

cornutum, *P. coronatum*, *P. mcallii*, *P. modestum*, *P. orbiculare*, *P. platyrhinos*, and *P. solare*. My phylogenetic reconstruction differs in several ways from the diagram published by Presch (1969:fig. 8). Presch depicted *P. asio* and the line leading to *P. braconneri* and *P. taurus* as arising independently from the ancestral *P. orbiculare* lineage. My cladogram has these taxa as branches off the same phylogenetic line. In Presch’s study, *P. ditmarsii* was considered a derivative of a *P. douglassii*-like lineage, a conclusion which I believe is no longer tenable. The resemblance of *P. ditmarsii* to *P. douglassii* is superficial, but *P. ditmarsii* agrees with *P. asio*, *P. braconneri*, and *P. taurus* in many details of the lepidosis (see Morphological Descriptions). Table 7 lists the synapomorphies linking *P. ditmarsii* with the southern radiation group. Moreover, in general habitus, *P. ditmarsii* is similar to *P. braconneri* and *P. taurus*, all three taxa having a shortened tail and elongate limbs (Table 9).

Another point of difference is the arrangement of northern radiation members having an “advanced maxillary” (=no contact between the nasals and maxillaries). Presch’s diagram has a polytomy and one line subdivides to yield *P. modestum* and *P. mcallii*. Presch (1969:274) regarded *P. modestum* and *P. mcallii* as “cognate” species, presumably due to the shared loss of the angular. Morafka (1977) reiterated the close relationship by referring to them as “sibling” species. The presence of the angular, however, is variable in *P. modestum*. Most computer manipulations of my data set place *P. modestum* with *P. platyrhinos*, and I conclude that the two species are each other’s closest relatives (siblings in the phylogenetic sense; Blackwelder, 1967:165). Both taxa form a sister group to *P. mcallii*, and in turn, all three species are the sister group of *P. solare*, producing a pectinate branching arrangement. None of these species can be considered siblings in the sense of being morphologically cryptic, since all are easily distinguishable by external characters.

The patristic distance tree (Fig. 14) depicts the amount of anagenetic evolution (based on the characters studied) that has occurred within the lineages of *Phrynosoma*. Members



Presch (1969) considered *P. orbiculare* to be osteologically the most primitive member of the genus, and he enumerated the ancestral states found in this species. In terms of both external and skeletal characters, my phylogenetic analysis places both *P. orbiculare* and *P. asio* as relatively primitive forms within their respective groups. *Phrynosoma asio* has an interesting combination of apparently plesiomorphic states, including narrow ciliary rows, some greatly depressed, enlarged dorsals in the median dorsal area, long second ceratobranchials, a steep postorbital orientation, a relatively long snout, two squamosal horns, vestiges of a lacrimal(?), a pos-

In phylogenetic systematics, the detection of homoplastic similarity is one of two recurrent problems, the other being the identification of ancestral character states. Homoplasy occurs when two taxa independently evolve the same character state. Both parallelism and convergence are subsumed in the concept. Convergent similarity between distantly related organisms is recognizable because the resemblance is superficial and never perfect. However, at progressively lower taxonomic levels, homoplasy becomes increasingly difficult to distinguish from homologous resemblance. Within the genus *Phrynosoma*, evolutionary trends have apparently led

to some striking examples of character convergence between members of the northern and southern species groups. The nature of the selective pressures producing this similarity, and the adaptive significance of the characters themselves, are not understood and subject to speculation.

The northern group members *P. cornutum*, *P. solare*, *P. mcallii*, *P. platyrhinos*, and *P. modestum* share with the southern species, *P. braconnierei* and *P. taurus*, similarity in several characters: 1) dorsal entry of the external nares (character ENAR); 2) location of the external nares well within (above) the canthal lines and slightly closer to the orbits (character PNAR); and 3) loss of contact between the nasal and maxilla (character NAMX). Presch (1969) referred to the last character as the "advanced maxillary" which he used to characterize the radiation of desert species in the northern group. The position and angle of entry of the external nares may be partially correlated characters. Also, the posterior displacement of the nares within the canthi may be developmentally correlated with the loss of contact between the nasal and maxilla (see discussion under External Naris). Configuration of the rostrifrontal region does not appear to determine narial position or contact between the nasal and maxilla. The northern group members mentioned above have an abrupt rostrifrontal angle, whereas the two southern group species, *P. braconnierei* and *P. taurus*, have more sloping profiles. A study of the possible functional significance of dorsally pierced nares, situated well within the canthi, seems warranted.

Coronoid overlap with the dentary and surangular (character CODS) is a primitive condition in *Phrynosoma*, and reduction or loss of this overlap has apparently occurred independently in both northern and southern species groups. Among members of the southern group, overlap is reduced in *P. taurus* and lost in *P. braconnierei*, while in the northern members, overlap is reduced in *P. modestum* and *P. platyrhinos*, and lost in *P. mcallii* and *P. solare*.

A supraorbital arch or bar (formed by the union of the prefrontal and frontal processes) has evolved independently at least twice, once in *P. taurus* of the southern group, and possibly once in the common ancestor of the northern species, *P. cornutum*, *P. solare*, and *P. mcallii*. The complete arch appears to strengthen the supraorbital area and to provide an additional brace for the superciliary spine, which otherwise is mainly supported by the postorbital. It is noteworthy, however, that *P. asio* usually has a narrowly interrupted arch (Table 3, Fig. 5), despite its long, projecting superciliary spines which are of apparent defensive importance in conjunction with the squamosal and parietal horns. Among the northern species, a complete arch was apparently secondarily lost in *P. platyrhinos* and *P. modestum*, perhaps as a consequence of an evolutionary trend toward crypticity for predator avoidance, rather than predator resistance based on spiny armament. I note that in both species the superciliary spines are reduced in size, and in *P. modestum* the dorsal spines are reduced and the abdominal fringe scales have become lost.

The presence of horns, especially on the parietal and squamosal elements, is one of the distinctive features of the genus *Phrynosoma*. The horns were presumably small in the com-

mon ancestor of the group, and subsequently enlarged in descendant species, perhaps in response to predator selection. However, in both northern and southern groups, there appears to have been a reversal in this trend. In the southern group, *P. ditmarsii* has parietal and squamosal horns that are remarkably reduced. Also in *P. taurus*, the parietal horns are quite small, but one of the squamosal horns has become greatly enlarged. Horn reduction has also occurred in the northern group member *P. douglassii*, a derivative of a *P. orbiculare*-like ancestor. Several races of *P. douglassii*, e.g., *P. d. douglassii* and *P. d. brevirostre*, have very small horns.

Surangular horns have evolved independently in the two species groups. In *P. ditmarsii* of the southern group, the surangular has several more or less ventrally directed horns. In the northern species, *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*, the surangular bears laterally directed horns. If the smooth surfaces of the frontal, jugal, postorbital, and parietal, seen in *P. asio* are truly retentions of the ancestral condition, then the tuberosities and other ornamentation present on these elements in members of both groups, must have evolved independently as well. The appearance of tuberosities and small horns on many of these elements may be viewed perhaps as a correlated evolutionary response to predator selection for enhanced spiny armament.

In sceloporines other than *Phrynosoma*, the maxilla is excluded from the orbital margin by the anterior process of the jugal. However, in most species of *Phrynosoma*, the maxilla may, to a greater or lesser degree, participate in the anteroventral border of the orbit. In the ancestral *Phrynosoma*, the maxilla was probably excluded from the orbit since that condition is seen not only in other sceloporines, but also in some specimens of several *Phrynosoma* species. Contact of the maxilla with the orbital margin has occurred independently in members of both groups within the genus. In *P. braconnierei* and *P. taurus* (southern group) the maxilla participates in the orbital border to a moderate extent, and likewise for the northern group species, *P. coronatum*, *P. douglassii*, *P. platyrhinos*, and *P. solare*. More extensive participation was noted in *P. cornutum* and *P. modestum* (Table 2).

The ectopterygoid is a slender element in sceloporine genera other than *Phrynosoma*. In horned lizards, with the exception of *P. orbiculare*, the element has become expanded anteriorly and shortened anterior to posterior. Parallel morphoclines were discerned in the northern and southern species groups (Fig. 15).

Another example of homoplasy concerns the supraoccipital, which in most *Phrynosoma*, has a nearly vertical orientation above the foramen magnum. In *P. taurus* (southern group) and *P. cornutum* and *P. solare* (northern group), however, the element arches posteriorly before joining with the parietal.

Homoplastic similarity involving the orientation and curvature of the postorbital has also been noted. In *Phrynosoma cornutum*, a northern group member, the postorbital tends to be oriented vertically and with limited outward curvature; a similar morphology characterizes the southern group members (Fig. 6).

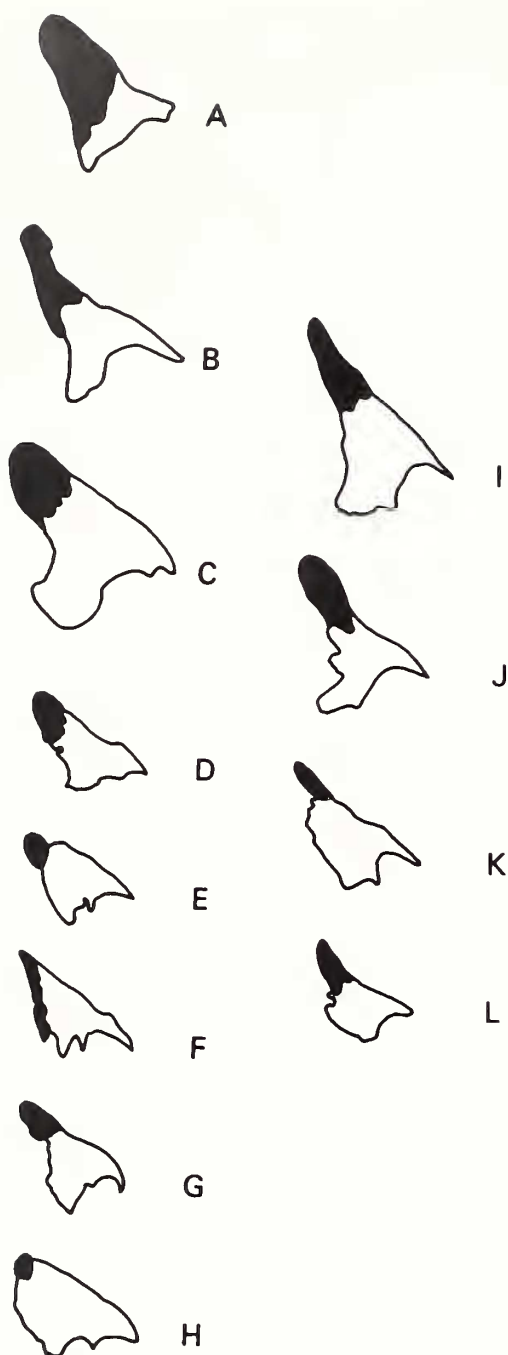


Figure 15. Evolutionary change in the shape of the ectopterygoid from a relatively long and slender, to short and wide element. Two parallel morphoclines A–H and I–L are illustrated. Darkened area represents inferior orbital fossa. Species are A, *P. orbiculare* (MVZ 137792); B, *P. douglassii* (AMNH 8237); C, *P. coronatum* (AMNH 73517); D, *P. cornutum* (AMNH 90804); E, *P. mcallii* (AMNH 73718); F, *P. modestum* (AMNH 74597); G, *P. platyrhinos* (AMNH 75472); H, *P. solare* (RRM 2324); I, *P. asio* (AMNH 74838); J, *P. ditmarsii* (UAZ 35511); K, *P. taurus* (UTA 17129); L, *P. braconnieri* (AMNH 90833).

Parallel trends in reduction of the second ceratobranchials appear to have occurred in the southern and northern species groups, but this conclusion is based on limited data (see discussion under Hyoid, and Fig. 7). *Phrynosoma ditmarsii*, *P. braconnieri*, and *P. taurus* have short or very short second ceratobranchials, a condition also seen in the northern species, *P. mcallii*, *P. modestum*, and *P. solare*.

The number of caudal vertebrae has undergone reduction independently in the northern and southern species groups. According to Presch (1969), *P. cerroense*, a derivative of a *P. coronatum*-like species, has a reduced number of caudal vertebrae, but his count of 19 falls within the range of variation of *P. coronatum* (14–23) (Presch, 1969:table 1, fig. 8). Several races of *P. douglassii*, notably *P. d. brachycercum* and *P. d. ornaticornum*, have a shortened tail (Montanucci, unpubl. data), and presumably a reduced number of caudal vertebrae. In the southern group, *P. ditmarsii* has about 14 caudal vertebrae, and this is further reduced (9–12) in *P. braconnieri* and *P. taurus*.

Most species of *Phrynosoma* have one or more rows of enlarged gulars on either side of the throat. A single row of enlarged gulars, or none at all, may have been present in the common ancestor. Three to five rows of enlarged gulars have, therefore, evolved independently in *P. coronatum* (northern group) and *P. asio* (southern group). In *P. platyrhinos* a single row may or may not be present, and in *P. modestum* the enlarged gulars were apparently lost. Enlarged gulars were apparently also lost in the *orbiculare* lineage. The trend toward loss is repeated in the southern group. *Phrynosoma ditmarsii* and *P. taurus* have a shortened row on either side, and in *P. braconnieri*, the row is further reduced or absent.

Homoplasy is also associated with the lateral abdominal fringe scales. The ancestral *Phrynosoma* may have had a single row of fringe scales, and if so, *P. asio* (southern group) and *P. cornutum* and *P. coronatum* (northern group) have independently evolved a second (lower) row of fringe scales. These several species are relatively large, conspicuous, spiny forms, and development of a second fringe row may have been correlated with the evolution of spiny armament through predator selection. *Phrynosoma mcallii*, *P. cerroense*, and *P. coronatum jamesi* have a short, lower row of fringe scales which may be viewed as secondarily reduced, considering that *P. cornutum* and most forms of *P. coronatum* have a fully developed lower fringe row. *Phrynosoma modestum* has completely lost the fringe scales, a possible consequence of evolution toward stone-mimicry (Sherbrooke and Montanucci, in press).

Finally, it is of interest to point out some morphological variations among the races of *P. coronatum* that are convergent with the morphology of *P. solare*. There is a tendency for the external naris to be situated slightly above the canthal line in *P. c. coronatum* and other Baja peninsular forms, as it is distinctly so in *P. solare*. The parietal shelf is extensive posteriorly in *P. solare*, and there is some development of a shelf beyond the limits of the occipital condyle in *P. c. coronatum*. In the northern *P. c. frontale* and *P. c. blainvillii*, however, the parietal is nearly even with the occipital condyle. The squamosal and parietal horns are markedly flat-

tened in cross section in *P. solare*. The horns are slightly flattened in *P. c. coronatum*, but in *P. c. frontale* and *P. c. blainvillii* they are nearly rounded. The squamosal and parietal horns are quite enlarged and flared in *P. c. coronatum*, the overall appearance being reminiscent of the encircling cephalic horns of *P. solare*. These parallels in horn morphology may be due to similarities in the kinds of predators and intensity of predation affecting horned lizard populations at southerly latitudes in the Sonoran–Sinaloan and Baja peninsular regions.

HISTORICAL PERSPECTIVE

My reconstruction of the phylogenetic history of *Phrynosoma* (Fig. 13) is an hypothesis based on the comparative distribution of character states among the extant species within the genus, as well as related, out-group taxa. A scenario for the evolutionary history of *Phrynosoma* is developed in the context of existing conceptual models of the paleogeography and paleoecology of North America (Axelrod, 1948, 1958, 1975, 1979; King, 1958, 1977). The chronology of geological events, following the time-scale of Berggren and Van Couvering (1974) and Van Couvering (1978), is used to estimate when the lineages of *Phrynosoma* may have separated. The fossil record of the genus is fragmentary and offers no empirical support for the branching topology of my cladogram. However, the fossil material is reviewed in an attempt to understand the relationships of some extinct forms, and to view the temporal distribution of extant species on the basis of fossils thus far accumulated. In the discussions that follow, there is a measured amount of hypothesis-fitting, which has risk since the existing paleoecological models, and their offspring, have not been subjected to rigorous evaluation. Furthermore, much of the geological history relevant to the evolution of *Phrynosoma* is a complex series of events for which detailed evidence is wanting. Therefore, my historical scenario for *Phrynosoma* is stated in general terms and provides only a basic framework which will undoubtedly be altered and refined as information about the paleoenvironment of North America accrues.

During the Eocene, the Neotropical-Tertiary geoflora was extensive in the southwestern region of North America. The epoch, however, marked the beginning of a gradual trend toward a cooler, drier climate. The tropical forests contracted southward and were replaced by a more diverse, drought resistant Madro-Tertiary geoflora. By middle Miocene, arid tropical scrub occupied much of the present Sonoran desert region and adjacent areas, and eastward, piñon–oak woodlands had spread through the uplands and nascent mountains of Mexico. Neotropical floras were confined to the south along the Pacific lowlands of Mexico (Axelrod, 1975, 1979).

The radiation of the sceloporines was probably directly associated with the development of the diverse Madro-Tertiary geoflora. Etheridge and de Queiroz (in press) conclude that *Phrynosoma* and the sand lizards separated from one another after *Petrosaurus* diverged from all other sceloporines and after the sand lizard–horned lizard lineage separated from that leading to *Sceloporus*–*Urosaurus*–*Uta*. Thus,

Phrynosoma may have diverged relatively late during the sceloporine radiation, possibly about late Oligocene–early Miocene. Sometime between early and middle Miocene, the ancestral *Phrynosoma* divided into two lineages. One lineage was an *asio*-like *Phrynosoma* which retained several primitive features, including a steep postorbital angle, an elongate snout, two squamosal horns, smooth frontal, jugal, parietal, and postorbital, non-peaked chinshields, a posteriorly narrow jugal, and possibly remnants of the lacrimals. This was a lowland form that may have inhabited arid tropical scrub and dry forest environments similar to those occupied by modern *Phrynosoma asio*. This lineage was to diverge from the ancestor by developing an expanded surangular with an angled edge, and keeled gular and ventral scales. The other diverging lineage, an *orbiculare*-like form, retained the primitive, convexly rounded surangular, relatively long, slender interclavicle median process, slender ectopterygoid, but diverged from the ancestor in having three squamosal horns, a low postorbital angle, a truncate snout, an expanded jugal, and small, but peaked chinshields. The *orbiculare*-like species occurred in upland environments (semiarid grasslands, and pine–oak woodlands) and was widespread by middle Miocene when the Mexican plateau and Sierra Madre Occidental and Oriental were uplifted (King, 1977). A nearly complete, fossilized maxilla of *Phrynosoma* from the middle Miocene (Split Rock Formation) of Wyoming was described by Robinson and Van Devender (1973) and questionably assigned to *P. douglassii*. The evidence would suggest that *P. douglassii*, or a form very similar to it (*P. orbiculare*?) was already in existence by that time, with a distribution extending to at least 42°N latitude. Murphy (1983) thought that Cascadian orogenic events at the end of the Miocene divided widespread populations into eastern and western halves, resulting in the formation of species pairs such as *Phrynosoma coronatum* and *P. orbiculare*, among others. Based on my cladogram, the two are not species pairs; a possibly more accurate interpretation is that the cladogenetic event at Node D (Fig. 13) corresponds to the late Miocene orogeny.

Phrynosoma coronatum or a *coronatum*-like progenitor gave rise to a series of five xeric-adapted species during the Pliocene and Pleistocene. Although the *coronatum*-like progenitor had enlarged chinshields, it lacked bony supports for them, but the desert forms that evolved from this lineage, evolved horns on the surangular and horns or protuberances on the dentary which support the chinshields. These desert species diverged further from the *coronatum*-like ancestor in having dorsally pierced external nares located well within the canthal lines, acquiring an abrupt rostrofrontal angle, and losing contact between the nasals and maxillae.

Phrynosoma cornutum is perhaps one of the earliest cladogenetic products of this small radiation of desert and semi-desert species. Fossils referred to *P. cornutum* are known from the upper Pliocene and were found in the Rexroad fauna (early Blancan Land Mammal Age; Oelrich, 1954), the Saw Rock Canyon fauna (early Blancan; Etheridge, 1960a), of Kansas and the Beck Ranch fauna (early Blancan; Rogers, 1976) of Texas, and the Sand Draw fauna (late Blancan; Holman, 1972) of Nebraska. Pleistocene and Holocene re-

mains of *P. cornutum* are known from Newton County, Arkansas (late Pleistocene; Gilmore, 1928), the Cragin Quarry fauna (Sangamon Interglacial; Etheridge, 1958, 1960b), the Nash Local fauna (Aftonian; Holman, 1979) of Kansas, Shelter Cave (late Pleistocene; Brattstrom, 1964), Dry Cave (late Pleistocene; Holman, 1970), Howell's Ridge Cave (Pleistocene–Holocene; Van Devender and Worthington, 1977), and Rocky Arroyo (early Holocene; Van Devender, 1980) in New Mexico, and the Slaton Local fauna (Pleistocene, Illinoian; Holman, 1969) and Hueco Mountains (late Pleistocene; T.R. Van Devender, unpubl. data) of Texas. *Phrynosoma cornutum* apparently evolved via allopatric speciation from a widespread population that was subdivided into eastern and western halves by further uplifting of the Sierra Madre–Rocky Mountains axis in the middle Pliocene (Eardley, 1962; King, 1977). Gene flow through the Cochise Filter Barrier (Morafka, 1977) was probably reduced prior to that time, allowing for gradual differentiation of eastern and western populations, and it may have ceased altogether with culmination of the middle Pliocene orogeny. The eastern population thus evolved into *P. cornutum*, while the western population became the progenitor from which *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare* arose. The western progenitor population was generalized in lacking a second pair of parietal horns, but probably shared a complete supraorbital arch with its eastern sister population.

Phrynosoma solare evolved a second pair of parietal horns and became ecologically associated with the Arizona Upland Subdivision (*Cercidium–Opuntia*) of the Sonoran Desert and with the Sinaloan Thornscrub (Brown and Lowe, 1980) to the south. *Phrynosoma mcallii* evolved from the western progenitor, possibly as a peripheral isolate or via parapatric speciation (Endler, 1977) when aeolian deposits were formed in the Salton Trough region. Middle Pliocene aridity probably enhanced the development of widespread sand habitats, allowing for the evolution of the distinctive dune-adapted morphology seen in *Uma* (Norris, 1958) as well as in *P. mcallii*. Thus, the evolution of *P. mcallii* may have commenced close to the time when the western progenitor became separated from the eastern progenitor of *P. cornutum*. *Phrynosoma mcallii* presently occurs on dunes formed during Quaternary time, largely from Colorado River delta sediment (Merriam, 1969), and on shell dunes along the Sonoran coast, perhaps of more recent geologic age (Ives, 1959). It also occurs in the sandy flats well inland from the coastal dunes.

A more recent (late Pliocene–early Pleistocene) derivative of the western progenitor population was a *platyrhinos*-like form which spread northward into the Great Basin, and eastward into the Chihuahuan desert during interglacial times. The lineage was characterized by loss of the complete supraorbital bar, and slight reduction of the chinshields to form more obtuse projections. The *platyrhinos*-like population may have become geographically isolated from the progenitor of *P. solare* and *P. mcallii* to the south, by the Colorado and Gila rivers. With increased precipitation during Pleistocene pluvial periods, a greater runoff would have occurred along these drainage systems (Schumm, 1965), and this may have created a more effective barrier to gene exchange than during

interpluvial periods. The *platyrhinos*-like progenitor was separated into western and eastern halves along the Cordilleran axis during the Pleistocene glacial periods, eventually resulting in the allopatric evolution of *P. modestum* from its sister, *P. platyrhinos*. These two *Phrynosoma* constitute east–west vicariant species pairs. Morafka (1977) listed a number of other vicariant pairs of amphibians and reptiles, but erroneously associated *P. modestum* with *P. mcallii*, and *P. platyrhinos* with *P. cornutum*. The role of the Cordilleran axis in the formation of east–west species pairs is quite clear, although their evolution may have occurred at different times. *Phrynosoma modestum* is known from the Cragin Quarry fauna (Sangamon Interglacial; Etheridge, 1958, 1960b) of Kansas. The locality is slightly farther north than the present distributional limits of the species (Conant, 1975). *Phrynosoma modestum* is also known from the extralimital locality of Deadman Cave, Pima Co., Arizona (middle Holocene; Mead et al., 1984; T.R. Van Devender, pers. comm.), as well as from Howell's Ridge Cave (Pleistocene–Holocene; Van Devender and Worthington, 1977) in New Mexico, and from Maravillas Canyon and Tunnel View, near Rio Grande Village (Pleistocene–Holocene; T.R. Van Devender, unpubl. data) in Brewster Co., Texas. A previously published record from Rocky Arroyo, New Mexico (Van Devender, 1980), proved to be a juvenile *P. cornutum* on reexamination (T.R. Van Devender, pers. comm.). The fossil record of *P. platyrhinos* is meager, with late Pleistocene and early Holocene material known from Gypsum Cave (Brattstrom, 1954) and Smith Creek Cave (Brattstrom, 1976; Mead et al., 1982) in Nevada. Pleistocene–Holocene fossils of *P. solare* are known from Deadman Cave (Mead et al., 1984) and Organ Pipe Cactus National Monument (T.R. Van Devender, unpubl. data), in Pima Co., Arizona. Norell (1983) described a new species of fossil *Phrynosoma* of late Neogene age, from the Anza Borrego desert of southern California. He indicated that only the fossil and *P. platyrhinos* and *P. mcallii* have two large parietal horns separated by a median, weakly pointed horn. However, this is incorrect as other *Phrynosoma* have the median horn (Presch, 1969:257). The fossil and *P. mcallii* have supratemporal fossae with flanges of bone emanating from their entire circumference. Norell (1983) considered this a derived character state, but he noted that the degree of bone encroachment into the fossae is more complete in *P. mcallii*. Occlusion of the supratemporal fossae is an ontogenetic process in *P. mcallii* (Norris and Lowe, 1951), and, therefore, I question whether this difference is real. The fossil also has accessory horns ventral to the enlarged squamosal horns, a feature apparently lacking in *P. mcallii* as well as other *Phrynosoma*. The morphology of the squamosal seems to be more derived in the fossil than in *P. mcallii* because of the unique presence of accessory horns. The fossil may represent a sister species to *P. mcallii*.

Phrynosoma holmani (Eshelman, 1975; Van Devender and Eshelman, 1979) is an interesting late Pliocene (late Blancan Land Mammal Age) fossil species, described from two right dentaries. The fossil material has a combination of ancestral and derived character states. The teeth are taller than extant species of *Phrynosoma*, with transversely expanded tooth

bases and weakly tricuspid crowns, a morphology suggesting a varied insectivorous diet (Van Devender and Eshelman, 1979). The dentary is also described by these workers as having a strongly angled ventrolateral surface, but apparently lacking protuberances. The angled dentary is a derived character state also seen in the assemblage of desert species *P. cornutum*, *P. mcallii*, *P. modestum*, *P. platyrhinos*, and *P. solare*. On the basis of this feature, *P. holmani* appears to be allied to this group. Furthermore, among other characteristics enumerated by Van Devender and Eshelman, are several which, in combination, suggest to me affinities with *P. cornutum*. These include: a depression on the posterior dorsolateral surface; an open Meckelian canal, with little constriction in the middle, and deep development of the dentary below the Meckelian canal. Van Devender and Eshelman concluded that none of the living species is apparently derived from *P. holmani*. However, I would suggest that *P. holmani* is a more primitive sister taxon of *P. cornutum*, or possibly near its ancestor, and was eventually displaced by the more derived species. Dentaries of Pleistocene *P. cornutum* and *P. holmani* are illustrated for comparison (Fig. 16).

Phrynosoma douglassii is a northern derivative of an *orbiculare*-like progenitor. The separation of these montane-adapted forms may have occurred at the start of the Pliocene when climatic drying began to outpace cooling, even at high elevations. With declining precipitation/temperature ratios, the forest biotas became contracted and fragmented, and the xeric Madro-Tertiary geoflora expanded to produce a desert continuum between the Mohave and Chihuahuan deserts (Morafka, 1977). This desert corridor through the Cochise Portal may have been sufficient to impede gene flow between populations along the north-south axis of the Sierra Madre-Rocky Mountains, thus resulting in the allopatric speciation of *Phrynosoma douglassii* from *P. orbiculare* or an *orbiculare*-like progenitor.

Phrynosoma adinognathus is a robust relative of *P. douglassii* from the early Pleistocene (early Irvingtonian Land Mammal Age) Borchers fauna of Kansas (Rickart, 1976). The description of this fossil is based on several fragments of dentaries and a frontal which are structurally robust, being several times thicker than *P. douglassii*. Rickart compared the fossil material with several hundred dentaries of sub-Recent *P. douglassii* and found the differences to be constant and without evidence of allometric increase of bone thickness with linear dimension. Rickart also indicated a larger size for *P. adinognathus* compared with *P. douglassii*. Van Devender and Eshelman (1979) compared this fossil form with extant material of *P. douglassii* of the same size, and suggested that the two may be found to be conspecific when the relationship between Pleistocene climates and robustness in reptiles and amphibians is better understood. However, Larry D. Martin (pers. comm.) doubts that the extreme robustness characteristic of *P. adinognathus* can be ascribed to Pleistocene climates as it is not seen in *P. douglassii* from glacial horizons (e.g., Type Sappa Locality, 1.2 million years B.P.). He is not aware of other examples of robustness aside from tortoises. Fossil material of *P. douglassii* is known from

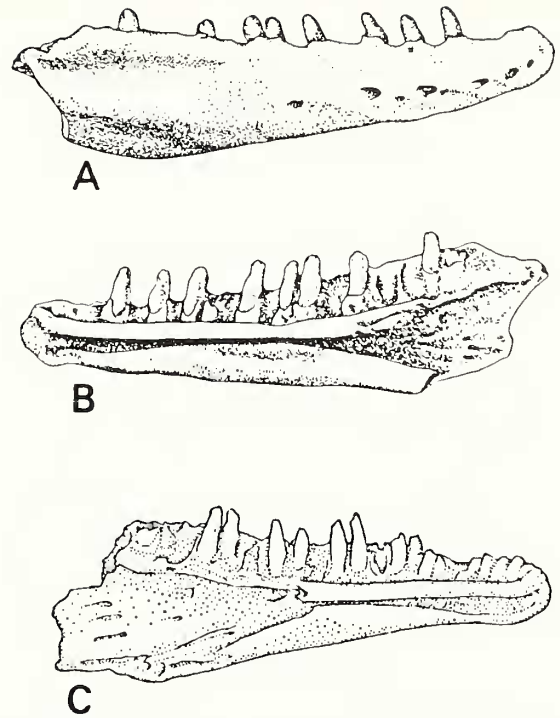


Figure 16. Dentaries of the late Pliocene *Phrynosoma holmani* (A, B) and Pleistocene *P. cornutum* (C). See text for discussion. Reproduced with permission from Eshelman (1975) and Holman (1979).

Deadman Cave, Arizona (late Pleistocene-early Holocene; Mead et al., 1984), Smith Creek Cave, Nevada (late Pleistocene, Wisconsinan-early Holocene; Mead et al., 1982), Burnet and Dark Canyon caves (late Pleistocene; Rickart, 1977; Wiley, 1972), Dry Cave (late Pleistocene; Holman, 1970), and Howell's Ridge Cave (Pleistocene-Holocene; Van Devender and Worthington, 1977), all in New Mexico, and from South Dakota (Pleistocene, early Kansan age; Holman, 1977), and from Pratt Cave (late Holocene; Gehlbach and Holman, 1974), Steeruwitz Hills (Pleistocene, late Wisconsinan; Van Devender, 1986 and unpubl. data), and Hueco Mountains (late Pleistocene; T.R. Van Devender, unpubl. data) in Texas.

Another extinct horned lizard is *Phrynosoma josecitense* of late Pleistocene (Rancholabrean Land Mammal Age) from San Josecito Cavern, Nuevo Leon, Mexico, described by Brattstrom (1955). Brattstrom indicated that this species, which has four squamosal horns, appears to be closely related to *P. solare*. Van Devender and Eshelman (1979) suggested, however, that *P. josecitense* may not be closely related to any extant species. I have examined a cast and photograph of the holotype and conclude that the fossil bears little resemblance to *P. solare*. Except for the presence of four squamosal horns, it differs in the shape and orientation of the horns. The internal shapes of the squamosal are similar to *P. coronatum* (Van Devender and Eshelman, 1979). The dorsal surface bears a small protuberance dorsal to and between the two posterior horns (Brattstrom, 1955). I find a similar protu-

berance between the last two horns in many *P. orbiculare*. There are only three squamosal horns in *P. orbiculare*, but a slight eminence on the posterior jugal may correspond to the most anterior horn in the fossil. However, in *P. josecintense* all the horns are situated on the same plane, whereas in *P. orbiculare* the eminence on the jugal lies slightly above the level of the squamosal horns. It is doubtful that the fossil specimen includes a portion of the jugal with the squamosal. The last two horns in the fossil curve slightly downward, a feature occasionally seen in *P. coronatum* and *P. orbiculare*. The two anterior horns on the fossil are quite dorsoventrally flattened and blade-like, a characteristic which I have not seen in the two aforementioned extant species.

Diversification of the *asio*-like progenitor, which produced *P. asio*, *P. braconieri*, *P. ditmarsii*, and *P. taurus*, appears to be relatively old, and probably preceded the radiation of northern desert species from a *coronatum*-like lineage. *Phrynosoma ditmarsii* from northern Sonora is disjunct and widely separated from its southern sister group (*P. braconieri* and *P. taurus*) which occurs in Guerrero, Puebla, and Oaxaca. When the adaptive radiation of this lineage took place is not certain, but orogenic events during the middle Miocene (King, 1977) may have provided the opportunity for the derivation of an upland (middle elevation) *Phrynosoma* characterized by long limbs, a shortened tail, and a viviparous mode of reproduction (note that viviparity evolved twice in the genus, once in this group, and once in the *P. orbiculare* lineage). The long-legged *Phrynosoma* is hypothesized to have had a latitudinally extensive distribution, but confined narrowly (between conifer woodland and thornscrub) along the western flanks of the Sierra Madre Occidental and regions south of the Transverse Volcanic Range. In the middle Pliocene, the Sierra Madre Occidental and Oriental, and Mexican Plateau, were further uplifted to near their present elevations (King, 1977; Eardley, 1962), promoting the spread of pine-oak and high-coniferous forests. The distribution of this long-legged *Phrynosoma* may have become fragmented into northern (*P. ditmarsii*) and southern (*P. braconieri*, *P. taurus*) remnants as a consequence of the renewed orogenic events. *Phrynosoma orbiculare* may have played a role in this displacement as its distribution now largely intercedes the northern and southern remnants.

Phrynosoma ditmarsii is presently associated with Madrean evergreen woodland (Lowe et al., 1971; Lowe and Howard, 1975) and short-tree forest, secondly Sinaloan Deciduous Forest (Perrill, 1983). *Phrynosoma braconieri* and *P. taurus* occur in arid tropical scrub and several montane habitats (pine-oak woodland and chaparral-oak forest; Davis and Dixon, 1961; Montanucci, 1979). The lowland *P. asio* is largely confined to arid tropical scrub and tropical deciduous forest (Davis and Dixon, 1961; Baur, 1979) from Colima and the Balsas Basin southward to northern Guatemala (Reeve, 1952; Duellman, 1958). Although *Phrynosoma ditmarsii* is widely separated from its southern relatives, it is possible that its distribution extends farther south than presently known. Suitable habitat apparently occurs beyond the

southernmost known locality near Tonichi, Sonora. There is also a possibility that a species of *Phrynosoma* phylogenetically intermediate between *P. ditmarsii* and its two southern relatives may still exist relictually in western Mexico. This putative species should be sought in a narrow zone south of the presently known ranges of *P. solare* and *P. ditmarsii*, and below elevations occupied by *P. orbiculare*.

Presch (1969) viewed *Phrynosoma orbiculare* as osteologically primitive and close to the ancestor from which all other *Phrynosoma* were derived. My analysis of the external and osteological characters indicates that both *P. orbiculare* and *P. asio* have each retained some of the primitive features originally present in the ancestor (see foregoing discussions). Thus both are relatively plesiomorphic within their respective groups. To derive *P. asio* directly from an *orbiculare*-like ancestor would require reversals to ancestral-like, apomorphic states for a number of *asio* characteristics: narrow ciliary rows; depressed median dorsals; non-peaked chinshields; steep postorbital; elongate snout; smooth parietal, frontal, jugal, and postorbital; two squamosal horns; and a posteriorly narrow jugal. To explain these character states as reversals would be less parsimonious than to consider them simply as retained primitive features of the common ancestor from which both *asio* and *orbiculare* were derived. The possible ecological implication of Presch's position could be that the presence of *P. asio* in tropical deciduous forest and arid tropical scrub habitats is the result of an invasion by a progenitor formerly living in a more temperate, xeric environment. In my opinion, something close to the reverse occurred during the Miocene, and the ecological setting of *P. asio* is in part similar to that in which the ancestral *Phrynosoma* existed. *Phrynosoma orbiculare* is unquestionably ecologically derived, being viviparous and adapted to relatively cool, dry, montane environments.

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APPENDIX

This list of specimens examined is presented alphabetically by taxon and museum (museum abbreviations follow Leviton et al., 1980). Specimens in the personal collection of T.R. Van Devender are designated TRV, and those of my personal collection are indicated by RRM; my collection will eventually be deposited in the LACM.

Callisaurus draconoides: AMNH 74592, KU 78521–23, LACM 130714, MVZ 79289–90; *Cophosaurus texanus*: CAS 9610–14; *Crotaphytus collaris*: AMNH 2363, 75090, 108314, KU 126925–27, MCZ 549, 131699; *Crotaphytus insularis*: AMNH 108972, KU 121464; *Gambelia wislizenii*: AMNH 73068, 75083, KU 121684–85; *Holbrookia elegans*: RRM 1620; *Holbrookia maculata*: RRM 1618; *Petrosaurus mearnsi*: CAS 143164, CAS-SU 17131–35, LACM 131520, MCZ 68900; *Petrosaurus slevini*: CAS-SU 17138–43, MCZ 85534; *Petrosaurus thalassinus*: CAS 101446–47, 119121, 154925–27, MCZ 14296, 68899; *Phrynosoma asio*: AMNH 18476–77, 18480–81, 18483, 19378, 46279–80, 62320, 62607, 68134–39, 72636, 74838–39, FMNH 31315, KU 40388–89, MVZ 137771, 137776, RRM 1754–57, 2333(7), TRV 1840–41; *Phrynosoma braconnieri*: AMNH 89669–72, 90833–34, 91483–84, 93808, 98086–87, 100731–32, 102746, 102748, 106817–21, FMNH 106208, KU 37761, MCZ 54959, 64101, MVZ 164361–63, USNM 47286, 111369, 165694, UTA 4222, 4348, 4588, 4594, 4837–40, 7732, 10281, 11391–94; *Phrynosoma cornutum*: AMNH 15403, 15416, 76188, 77051, 77117, 90804, 99686, FMNH 31311, 31339, 98392–93, KU 2099, 7231, 7233, 13940, 18202, 19372–75, 19377, 19387, 19405–10, 19429, 19444, 19447, 19554, 20992–93, MCZ 508, 511, 4555, 37217, 169686–87, 169857, MVZ 78385–87, 137667, RRM 2088–97, 2109–11, 2118–20, 2124–25, 2207–08, 2264, 2309, 2334–35, 2337, 2358, UMMZ 149114–16, USNM 20956, 194855–56, 220237–41; *Phrynosoma cor-*

onatum: AMNH 5148, 73517, 77049, 77052, 94547–48, 95068, 99685, CAS 58152, FMNH 22394, 98954, LACM 127268–69, MCZ 5515, 131759, MVZ 272, 58181, 137775, 13777–82, RRM 2029–34, 2176–78, 2331–32, 2347, 2369–75, 2395, 2398, UMMZ 169885, USNM 220242–43; *Phrynosoma ditmarsii*: AMNH 557, 107380, 112381–83, MVZ 134105, RRM 2392, 2399, 2400(3), 2401(3), 2402–03, 2408, 2409(6), 2412, TRV 2535–37, UAZ 35511, USNM 36013, 36022; *Phrynosoma douglassii*: AMNH 8237, 70639, 77050, CAS 34706, FMNH 98394, KU 13943–45, LACM 4342–53, 19654–66, 19680–93, 25386, 26969, 62556–57, 101534–35, 101539–51, 101557–58, 107275, 111228–31, 113428–41, 123341, MCZ 5280, 9165, 62485, 139423, MVZ 58199, 77046, 82664, RRM 2265, 2306, 2310, 2389, UMMZ 138823, 149118–20, USNM 135990, 220244, 222978; *Phrynosoma mcallii*: AMNH 31811–12, 60571, 66052, 73718, 77041–48, 84487, 108301, 125771, FMNH 216162, KU 6998, 21930–31, MCZ 44822, 61473, MVZ 1006, 111509, RRM 2236–42, 2346, 2397; *Phrynosoma modestum*: AMNH 1323, 1327, 74499, 74597, 85624, KU 473, MCZ 62288, RRM 2073–87, 2288–95, 2313, 2342, 2396, UMMZ 149121; *Phrynosoma orbiculare*: AMNH 15423, CAS 156548–49, 156561, KU 23746–48, 25852–82, 25884–86, 28067, 29799, 40386–87, 44163–64, 51764, 92571, MCZ 11313, 19560, MVZ 137792, RRM 2377–79, USNM 220245; *Phrynosoma platyrhinos*: AMNH 547, 68612, 75472, 77039–40, 77053–

55, 108316, CAS 40788, FMNH 31289, 216163, KU 22237, LACM 127270, MVZ 1300–01, 58573, 64187, 79295, RRM 2039–45, 2126, 2128–29, 2166, 2323, 2367–68, 2394, 2407, UMMZ 149122–28, 169878, 169884, 169888, USNM 220246; *Phrynosoma solare*: AMNH 1285, 2579, 70095, 72477, 84561, FMNH 22415, 98395–96, KU 13941, MCZ 10008, MVZ 79601–02, 95986, RRM 2098–99, 2101–02, 2108, 2127, 2319, 2324–25, 2328–29, 2336, 2376, 2405–06, UMMZ 180454, USNM 220247; *Phrynosoma taurus*: AMNH 72530, 102749, CAS 139841–42, 141361, 154069–70, FMNH 105464, KU 37802, MCZ 43284, MVZ 45004, RRM 2235, UMMZ 88640, USNM 46713, 111368, UTA 4841, 9092, 11388–90, 11395, 17129; *Sator angustus*: CAS 52481–84, CAS 52486, 52499; *Sator grandaevus*: CAS 148912–17; *Sceloporus graciosus*: LACM 131567–68; *Sceloporus grammicus*: LACM 129272, 129950–51; *Sceloporus merriami*: CAS-SU 9884; *Sceloporus occidentalis*: AMNH 107494–95, LACM 129634, 134420, 135428, MVZ 4785, 39223; *Sceloporus parvus*: CAS 115871–76; *Sceloporus undulatus*: KU 40322–23, LACM 127273–75, 127340; *Sceloporus variabilis*: MVZ 81313–14; *Uma notata*: AMNH 68847, CAS 55368–69, 53371; *Urosaurus auriculatus*: LACM 132546–47; *Urosaurus graciosus*: CAS 45335–40; *Urosaurus microscutatus*: CAS 146814–19; *Uta stansburiana*: LACM 127271, 130719–20, MVZ 78200–01, RRM 1638.